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THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS

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THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS

THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS[1]

SARKIS BOSHNAKIAN[2]

The mendelian inheritance of each of the more striking characters in wheat, such as beardedness, color, felting, density, and so forth, has been determined qualitatively by various workers. Much remains to be done, however, if the genetics of these characters is to be analyzed from a quantitative point of view, as there are numerous lesser inherited variations within their simple gross segregations.

Practically all of these characters show certain degrees and types of interrelations with other characters. Some of them show complete or partial linkage. Others, when analyzed quantitatively, appear to have been affected by one or another character but not necessarily linked with it, so that if one of these characters appears in an intense or a dilute form the others vary also in the same direction and more or less in the same degree.

Besides the above-mentioned type of interrelation, in which the appearance and the intensity of appearance of a group of characters are due to the presence or the absence of the same factor or factors, there is another type embracing a set of characters that appear as an indirect effect of the presence of another character. In a sense these characters are acquired, but they seem to be inherited simply because the causal character is inherited; and whenever the latter is present it gradually causes the modification of the former characters during the lifetime of the individual.

The subject of the inheritance of types of internode length presented in this paper has been treated from the following three viewpoints: (1) the analyses of minor segregations within gross (3 : 1, 1 : 2 : 1, or the like) segregations; (2) the determination of the interrelations of varied

[1] Paper No. 93, Department of Plant Breeding, Cornell University, Ithaca, New York. Also presented to the Faculty of the Graduate School of Cornell University, March, 1920, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] In cooperation with the Office of Cereal Investigations, United States Department of Agriculture.

characters; and (3) the determination of characters that were found to be the resultant of other characters.

Since the characters studied were confined to those that were not distinctly contrasting in the usual mendelian sense but represented different gradations on a scale between two extreme quantitative characters, it was not possible to classify them into genetic classes or to express the results always in terms of ratios. The analyses were made according to such biometrical methods as seemed best suited to bring out the directions and tendencies of the variations. Factorial explanations, however, have been given wherever the facts obtained warranted the formulation of such hypotheses.

The material on which observations were made consisted, exclusive of interspecific crosses, of more than sixty F_2 progenies, fourteen of which were carried through the F_3. To avoid duplications of similar results it is not considered necessary to present here the results of all the crosses, but sufficient data are given to serve as illustrations and to show the general trend of the various modes of inheritance.

For many valuable suggestions and criticisms during the progress of this work the writer fully acknowledges his indebtedness to Professor H. H. Love, of the Department of Plant Breeding at Cornell University, under whose direction the studies were made. Most of the F_2 and F_3 progenies studied were furnished by Dr. C. E. Leighty, of the United States Department of Agriculture. The writer wishes to express his appreciation of Dr. Leighty's generosity in supplying these and also carefully numbered hybrid progenies, which made possible the tracing of each back to the F_1 and parental material, all of which had been saved. Thanks are due also to the Office of Cereal Investigations, United States Department of Agriculture, through whose courtesy the writer was enabled to enjoy the field and laboratory facilities at the Arlington Experimental Grounds during the summers of 1916 and 1917.

PHYSIOLOGICAL CONDITIONS AFFECTING RACHIS INTERNODE LENGTH

Like many quantitative characters, density and squareheadedness are affected to a greater or less extent by a number of environmental conditions which tend to change the normal course of development of the plant, thereby suppressing or accelerating the growth of certain of its

parts. A brief discussion of the effect of environmental factors on the production of these internode characters will serve to show to what extent nongenetic variations may take place. In the first part of this paper the main object is to explain the phenomena of density and squareheadedness on a purely mechanical basis.

DETERMINATION OF DENSITY AND OF SQUAREHEADEDNESS

The terms *density* and *squareheadedness* are used in this paper to designate two different phenomena of rachis internode length. The differences between these two characters are discussed elsewhere (Boshnakian, 1917)[3], but they may be briefly redescribed here.

Density is expressed in terms of average rachis internode length, which is found by dividing the length of the rachis by the number of rachis internodes. The average internode length, or density, of a head 90 millimeters long with 20 rachis internodes, is thus 90 ÷ 20, or 4.5 millimeters. The average internode length in wheat varies from about 1.3 to about 8 millimeters. In *vulgare* wheat it usually does not extend beyond 5 millimeters. Density is comparative.

The average internode length usually varies in dense wheats from 1.2 to 2.5 millimeters, and in lax forms from 3 to 5+ millimeters. There are intermediate gradations, but, in a general way, by *dense* or *lax* forms are meant, respectively, forms varying in density between the two ranges specified. Although the word *club* refers to a capitate type of head, following the present usage of this term it is here applied to dense wheats of the *sativum* group (that is, *Triticum compactum*) whether capitate or not.

Squareheadedness, on the other hand, refers to the ratio between the average internode length of the central third of the rachis and that of the terminal third. The density of the middle and upper thirds of the rachis is equal to the ratio of the number of internodes in these two sections of the rachis. The coefficient of squareheadedness is found by dividing the number of rachis internodes in the terminal third of the rachis by the number of internodes in the middle third. Thus, if the terminal third has 9.5 internodes and the central third has 5.6 internodes, the degree of squareheadedness is equal to 9.5 ÷ 5.6, or 1.69. The forms

[3] Dates in parenthesis refer to *Literature Cited*, page 881.

that are usually called *squareheads* have a coefficient of about 1.33 or more; and in this paper, by *vulgare* or *non-squarehead* forms are meant types with coefficients of less than 1.33, and by *squareheads*, forms having coefficients of more than 1.33. This division is entirely arbitrary and is made for convenience.

It is seen, then, that squareheadedness has no reference to density. Squareheads may be dense or lax. This divides the wheat types into the following four classes with respect to their rachis internodes: non-squarehead, lax (*Triticum vulgare*, Plate LXVII, upper, 12); squarehead, lax (*Tr. capitatum*, Plate LXVII, upper, 11); non-squarehead, club (*Tr. compactum*, Plate LXVII, lower, 13); squarehead, club (*Tr. compacto-capitatum* Plate LXVII, upper, 9). These varietal names apply to the wheats of the *sativum* group only.

According to these classifications, the semi-dense forms having a squareheadedness of less than 1.33 are named *semi-dense vulgare*—not *squareheads*, a name too often applied for such forms, and perhaps with some justification as such semi-dense forms when well developed may appear square in cross section.

Since the discussions in this paper center solely upon squareheadedness and density, it is necessary for the reader to bear in mind the sense in which these two terms are used.

DEVELOPMENT OF THE WHEAT PLANT WITH REFERENCE TO SQUAREHEADEDNESS

The head of the wheat plant is found in an embryonic stage when the plant starts a new growth after a short or a long period of rest. When the head is about 10 millimeters long it is covered with concentric rings of sheaths, each sheath being attached to the culm at its respective node. The different parts of the plant do not all grow at the same rate.

When the spike is about 15 millimeters long, the enveloping sheaths and blades are fairly well developed, but the culm internodes are only a few millimeters in length, the terminal ones being the shortest. After the sheaths have gone through their chief period of growth, the development of the internodes is accelerated. During this period the head also begins to develop. From this time on, the increase in the height of the

VARIOUS FORMS OF GROWTH

Upper: 1, *Aegilops ovata:* 2, F_1 (Aegilops x Silver Club); 3, Silver Club. 4, White Spelt; 5, Dale Gloria; 6 to 12, F_2 types (White Spelt x Dale Gloria, series 13255a)— 6, homozygous lax spelt; 7, heterozygous dense spelt. 8, homozygous dense spelt; 9, homozygous dense *sativum* (club); 10, heterozygous dense *sativum;* 11, homozygous lax *sativum,* squarehead; 12, homozygous lax *sativum, vulgare*

Lower: Dense forms of different species: 1, *durum;* 2 and 3, capitate and dense barley heads (lateral florets of 2 removed); 4, capitate *sativum;* 5, dense spelt; 6, dense *polonicum;* 7 and 8, club wheats; 9, *turgidum;* 10, club; 11 and 12, capitate *dicoccums;* 13, club pyramidal; 14, capitate spelt; 15, dense *polonicum;* 16, club

VARIOUS FORMS OF GROWTH

Upper: 1 to 5, 6 to 10, Heads of two hybrid plants showing lack of harmony of growth characters. 11 and 12, Heads of spelts subjected to longitudinal pressure; zigzagging of internodes produced instead of squareheadedness

Lower: 1 to 4, 5 to 8, Heads of two plants showing variations in density on same plant; plants grown in greenhouse; long spikes headed out about four weeks earlier than dense spikes

plant is due primarily to the increasing length of each culm internode. During the first period of the development of the culm, the basal internodes, except a few near the ground, begin to develop, and successive internodes undergo their chief period of growth as the growth of the internode below is beginning to decline. The terminal section of the culm, which carries the spike, during its development has to push the spike up all along the length of the terminal sheath, which envelops the head in such a way that occasionally, and especially among plants of hybrid origin, the culm cannot exert sufficient pressure to unfold the sheath. In such cases the spike fails to head out; or, if it finally does head out, the head appears in an abnormal condition and the tip spikelets very often remain undeveloped (Plate LXVIII, upper, 1 to 10).

The factors that seem to produce a strain on the terminal culm internode during its growth are the following: the rapid growth of the culm; the spread, width, shape, and texture of the spikelets; the stiffness of the enveloping sheath and its resistance to unfolding.

It seems that as the rate of growth of the terminal culm increases, the movement of the spike through the sheath should encounter a greater degree of resistance in an opposite direction.

The spread of the spikelets is probably one of the most important factors. The glumes of the spikelets are pointed upward and outward. This in itself tends to increase resistance. If the contact of the glumes with the sheath increases their spread, the resistance will increase many fold. In species such as the spelt or the emmer, in which the spikes are very narrow and the spikelets are very close to the rachis, the resistance is decidedly decreased because the spikelets themselves assume a wedge shape, the glumes being drawn together tightly; and also because the spikelets, lying flat against the rachis, are not likely to spread out.

The third factor, which is not so important as the other two, is the texture of the sheath and its habit of development. The sheath that normally unfolds at the proper time, or is easily unfolded by the movement of the spike, sometimes fails to open completely or opens under difficulty. Sheaths of this type produce a considerable longitudinal pressure on the culm.

THE MECHANICS OF SQUAREHEADEDNESS

In order to understand the mechanics of the production of squareheadedness, it is necessary to know the effect that is produced by pressure along the culm axis. The presence of longitudinal pressure is evident from the undulations of the culms often observed in square or dense forms (Plate LXVII, lower, 9 and 10.) The part of the spike that most reacts to the effect of pressure is the terminal part, because it is directly in contact with the sheath. The pressure produces a compressing effect, and this in turn checks the development of the terminal part of the head, especially the development of the rachis internodes, and produces the effect known as squareheadedness.

This character of squareheadedness is mainly evidenced by the gradual shortening of the terminal rachis internodes (Plate LXVII, lower, 4, 11, and 12). But there are also other characters which accompany this shortening of the internodes and which are the direct or indirect results of the same cause. One of the most prominent of these is the so-called clubbing, or capitate form, produced by the spreading of the spikelets away from the rachis in those regions of the head where the internodes are short. Because of the pressure exerted, the normal elongation of the internodes is inhibited but the spikelets in most cases continue to develop. Since the space between the spikelets is not sufficient, they are forced mechanically to spread out to make more room for development. This process is on the principle of the isosceles trapezoid, in which, the base being constant, the distance between the sides increases as the latter take a position toward a right angle with the base. In the plant the rachis internode is represented by the base, and the axes of the spikelets by the sides, of the trapezoid.

In squareheads the spikelets of only the upper part of the spike (except the terminal two or three spikelets) thus diverge. In most *compactum* forms all spikelets diverge as a result of the shortness of all the internodes. This is seen on comparing the divergence of spikelets of dense heads 5 and 9, in Plate LXVII (upper), with that of lax heads 2, 4, and 6. In wheat, as well as in barley, the opposite condition exists also in some cases; that is, the shortening of the internodes does not occur near the upper part, but near the basal region. In such cases the ear, in-

stead of being capitate in form, assumes a pyramidal or conical form, as shown by heads 13, Plate LXVII (lower), and 8, Plate LXVII (upper).

Another phenomenon of squareheadedness is the drawing of the terminal spikelets toward one side so that when the head is viewed along one of the directions of the plane of symmetry, which separates the spikelets of one side from those of the other, the rachis appears exposed (Plate LXVII, upper, 11). Viewed from the opposite side the rachis is covered by glumes and awns which are outdrawn and gathered in that direction. With the receding of the glumes the part of the side where the rachis is exposed appears flat (Plate LXVII, upper, 11), and to a person not viewing the head from the opposite side also it gives the impression that the spike is square in cross section. This impression, which has been left on the popular mind, has given to this form the name *squarehead.*

The character of squareheadedness is not confined to the wheat known by this name but may appear also in the dense forms known as club wheats (*Triticum compactum*). The total shortening of rachis internodes in these forms is primarily due to the presence of a genetic factor which produces also a general shortening of many parts of the plant. But in most forms a certain degree of squareheadedness may be found. This may be inherent—that is, transmissible—or it may have been produced mechanically. When the spikelets spread out as a result of the shortness of the internodes, as described above, the increased width of the head and the projections of the tips of the glumes are likely to offer considerable resistance, thus producing squareheadedness in the manner already explained.

EFFECTS OF CROSSING ON SQUAREHEADEDNESS

Squareheadedness, and shortening of all the rachis internodes, are two different phenomena. As shown in the preceding discussion, squareheadedness is a postnatal character, as it were, being dependent on the combined effect of certain vegetative growth characters. Density of the *compactum* wheats, on the other hand, is predetermined and is due to the presence of one or more genetic factors which cause dwarfing of a number of plant parts, including incidentally the shortening of all rachis internodes.

Squareheadedness is dependent on a certain balance of the rate of

growth of the parts concerned. An unfavorable balance produced through hybridization may result in certain hereditary anomalies. A few such forms are shown in Plate LXVIII (upper). Heads 1 to 5 were produced on a single F_2 plant derived from a cross between a *durum* and a common wheat. In these cases the curling of the awns all along the length of the heads shows that the latter were partly prevented from moving up the sheaths by the tightening of the sheaths. The illustrations show also the rudimentary condition of the terminal 5 to 7 spikelets, which represent the region whose growth was checked altogether by being subjected to pressure.

Heads 6 to 10 in the same plate represent another condition of lack of harmony of growth between different parts of the plant. The spiral form of the awns of head 7 shows that this head was forced to make a corkscrew movement while making its way up the sheath. Heads 8 and 10 show the failure of the sheath to open at the proper time. Heads 6 and 9 represent heads that were finally released.

Heads 11 and 12 represent a single spelt plant whose sheaths were evidently wrapped too tightly around the heads. The pressure which the tight sheath exerted on the head by the growth of the culm produced a zigzagging of the rachis. The internodes of the spelts, being comparatively stiff, are not so likely to remain short as a result of pressure.

These two spelt heads are interesting because they show the relative tendency of the different internodes to be affected by pressure. The basal internodes are thick and are very slightly affected by the induced zigzagging effect. Each successive internode is weaker than the one below, and more and more likely to show the effect of pressure. The conditions to which these heads were subjected are identical with those to which squareheads of *sativum* or other soft-glumed species are subjected, but the effect is somewhat different because of the differences of texture and ear form of the spelt as compared with those of some other forms.

These cases show that there are a number of growth characters to which the production of squareheadedness is due, and that the factors producing these characters seem to segregate and recombine like any other factors. If the combination is such as will produce a pressure of

the head in a certain rate and intensity, various degrees of squareheadedness may result. If the head encounters little or no pressure the internodes may be more or less uniform, and if the growth of parts is unbalanced certain abnormalities of the spike may result.

Since a number of morphological factors are concerned in the production of squareheadedness, logically it would be expected, and experimentally it would be found, that the segregates of a cross between a squarehead and a non-squarehead do not appear in a definite ratio but give a distribution approaching the normal curve of error.

EFFECTS OF NUTRITION

In one of the preliminary experiments to determine the effect of nutrition under field conditions, seeds from a pure variety of a squarehead were grown at varying distances. In one case the seeds were drilled rather closely; in the second case they were planted 7.5 centimeters apart; in the third case they were planted 15 centimeters apart. The frequency distribution of squareheadedness of these three sets of plantings is given in table 1. The set that was drilled in had a mean degree of squareheadedness of 1.325 ± 0.012; the seeds planted 7.5 centimeters

TABLE 1. VARIATIONS OF SQUAREHEADEDNESS IN PLANTS GROWN AT VARYING DISTANCES
(Variety, Giant Squarehead)

	Squareheadedness													Number of plants	Mean
	1.00	1.10	1.20	1.30	1.40	1.50	1.60	1.70	1.80	1.90	2.00	2.10	2.20		
Seeds drilled	1	14	18	25	19	3	10	2	..	2	..	..	..	94	1.325±.012
Seeds planted 7.5 cm. apart	..	..	1	..	8	3	10	7	3	3	2	4	1	42	1.678±.025
Seeds planted 15 cm. apart	..	2	6	..	2	..	1	..	..	..	..	..	..	11	1.254±.027

apart gave a higher mean, 1.678 ± 0.025; and those planted 15 centimeters apart gave a mean of but 1.254 ± 0.027.

The plants from the drilled rows made a fair growth but were inferior to those of the second set. The plants of the third set were mostly winterkilled, and such as survived had a poor stand with heads of varying length and degrees of development. The poor condition of the last-named was due to the wide distances between the plants, which made them unable to protect themselves from winter conditions. In the case of the other sets there was enough foliage developed during the fall for winter protection.

Disregarding the third set, it is apparent that the high degree of squareheadedness of the second set was due to the greater feeding allotted to these plants; for there was also a corresponding general development.

Another experiment was made with potted plants growing under greenhouse conditions. It consisted of four sets of nine pots. One set was grown in a cool house, the second under moderate greenhouse conditions, the third in a damp chamber, and the fourth in a rather warm place. Each set consisted of triplicate pots containing, respectively, soils of a very poor sandy mixture, of fair fertility, and of higher fertility.

In the sets grown in cool and moderate temperature conditions, the pots containing poor soil produced heads of a low degree of squareheadedness, while the heads of plants grown in moderately fertile soils showed a higher degree of squareheadedness.[4]

There is no question that in these cases the high degree of squareheadedness was produced by the fertility of the soil. That fertility increases squareheadedness has been noted by Edler (1903), Preul (1908), Ohlmer (1908), and Meyer (1909). Meyer found in addition that nitrogen was the causative factor, as neither calcium, potassium, nor phosphorus, alone or in combination, had any noticeable effect on the production of this character.

It is not so difficult to explain how high fertility increases squareheadedness, in the light of the causes of squareheadedness given in the preceding discussions. If rapid growth of the culm subjects the head to higher pressure, the spike takes the squarehead form. By increasing the nitrogen content of the soil, the rate of growth of the culm is accelerated and the tissues of the parts of the head are softened. The first of these conditions increases the pressure to which the head is subjected, and the second renders the head more sensitive to the effect of pressure. In the absence of sufficient nitrogenous food, the rate of growth is retarded and the parts of the head become fibrous. Due to the first condition sufficient pressure is not developed, and with the hardening of the tissues the spike offers a greater resistance to whatever pressure may be developed.

[4] The sets grown in the damp chamber and in the warm place did not do well.

The effect of the rate of growth on squareheadedness may be determined also by ascertaining the degree of squareheadedness of the leading culm and of those that develop later. Practically in every case the leader, which is by far the most vigorously growing culm, has a higher degree of squareheadedness than the others. Often the smaller culms of squarehead plants will have *vulgare*-like heads.

In cases in which squareheading is increased by the rapid growth of the culm, the plants having longer spikes are more squareheaded than those with shorter spikes. The relative degree of squareheadedness of short and of long spikes of the same plant is shown in table 2. From four to six well-developed heads were measured from each plant in connection with another experiment. Here the shortest and the longest of these, respectively, are shown. Out of twelve cases taken at random there was but one case in which the short head had a higher degree of squareheadedness. The average of the summation of the differences was 0. 17 ± 0.021 in favor of the long heads.

TABLE 2. DIFFERENCES IN DEGREE OF SQUAREHEADEDNESS OF LONG AND OF SHORT HEADS OF THE SAME PLANT

Short heads		Long heads		
Length (centimeters)	Squareheadedness	Length (centimeters)	Squareheadedness	Difference in squareheadedness
10.0	1.23	13.5	1.47	+0.24
11.6	1.41	13.2	1.51	+0.10
10.4	1.50	13.8	1.50	0.00
10.3	1.24	12.0	1.51	+0.27
10.7	1.21	14.0	1.37	+0.16
10.5	1.24	13.6	1.48	+0.24
8.0	1.39	10.5	1.60	+0.21
7.6	1.31	10.0	1.65	+0.34
8.7	1.51	10.1	1.65	+0.14
8.4	1.33	11.2	1.57	+0.24
8.3	1.39	12.5	1.58	+0.19
7.9	1.29	10.3	1.17	−0.12
Mean and average error				
9.4 ± .35	1.34 ± .025	12.0 ± .40	1.50 ± .026	+0.17 ± .021

When vigor is induced by soil fertility, the plants with longer heads will be more squareheaded than the others; and when vigor is induced by crossing certain *vulgare* forms, the long heads of each plant will be found to be more of a squareheaded type. The increase of squareheadedness of the F_1 plants, as shown later, will serve as examples.

If, on the other hand, squareheadedness is caused, not so much by the

vigorous development of the culm, but by the failure of the sheath to unfold at the proper time, then the plants that are more squareheaded will be found to have shorter heads that the non-squarehead forms. Figures illustrating this type of squareheadedness are given in connection with the discussion of that subject.

Before concluding the discussion of the effects of nutrition, it may be well to make a few remarks regarding its effect on the density of the *compactum* form. As already mentioned, the density of this form is not the result of pressure. But by increasing the fertility of the soil it is possible to change markedly the degree of density. Four heads from each of two *compactum* plants are shown in Plate LXVIII (lower). These two plants were grown in 4-inch pots in a greenhouse. The soil was highly fertilized. The heads first developed (2, 4, and 5) were almost like *vulgare*, but as the season advanced, and more spikes began to head out, the heads became more and more dense. There was an interval of about four weeks between the time of heading-out of the first and of the last head. When the last spike headed out, the first one was almost ripe—that is to say, the nutrients in the plant or those in the soil were already used up; hence the spikes heading out later obtained very little food. From the difference in thickness of the culms of dense and lax heads an idea may be formed of the relative amount of nourishment obtained by the different heads.

This experiment was conducted under abnormal environmental conditions, and it is not likely that variations as great as these will be found on plants growing under field conditions. But it points out the fact that increased fertility in the soil tends to increase the length of the rachis internodes.

SUMMARY

The wheat plant during its development undergoes two more or less distinct periods of growth. In the first period the sheaths and the blades develop. In the second period the rate of growth of the sheaths diminishes and the culms begin to develop, and during this period the spike carried at the end of the terminal culm internode is pushed up through the enveloping sheath.

Squareheadedness is the combination of a number of characters which

are produced by the shortening of the terminal rachis internodes. It is expressed by the coefficient found by dividing the number of internodes in the terminal third of the rachis by the number of internodes in the central third.

Density is the shortening of all the rachis internodes. It is determined by dividing the length of the rachis in millimeters by the number of internodes.

There are numerous gradations of squareheadedness and of density.

Squareheadedness is the result of pressure developed by differential growth of culm and sheath.

Rapid growth of the culm, failure of the sheath to unfold, and ears with soft-spreading glumes, tend to increase squareheadedness.

Any factor, genetic or environmental, which affects principally the development of the above-named characters, will affect the degree of squareheadedness.

Fertility of the soil or access of the root system to sufficient available nitrogenous matter increases squareheadedness.

Density is purely an inherited character, but favorable growth conditions may somewhat increase average internode length. Under abnormally favorable or unfavorable conditions, the increase or the decrease of density even on the same plant may be considerable.

THE GENETICS OF SQUAREHEADEDNESS

Investigations on the genetics of squareheadedness have given many confusing results, chiefly because no definite standards have been used for measuring this character. There are many instances in which this word has been used for designating a moderate degree of density.

One of the earliest studies of the subject was made by Rimpau (1891), who crossed lax *vulgare* types with lax and moderately dense squareheads. The F_1 hybrids were intermediate and the types of the F_2 populations varied within respective parental ranges.

Von Rümker (1909) obtained from squarehead x *vulgare* crosses, F_2 populations, some of which yielded more and others fewer squareheads. The squareheads varied also in degree.

Nilsson-Ehle (1911) found the *vulgare* type to be dominant over the

squarehead form. The ratio of *vulgare* to squarehead was between 3:1 and 15:1.

Further work has been done, but because of the different meanings given to the word *squarehead* it is not possible to compare the results with those that are here presented.

INHERITANCE OF SQUAREHEADEDNESS IN CROSSES WITHIN THE SATIVUM GROUP

Squareheadedness is a quantitative character. Crosses in which it is involved do not show a clear-cut segregation into mendelian classes and ratios. Physiological experiments have shown that the character is the result of the interaction of a number of growth factors, certain combinations of which cause the compacting of the terminal part of the spike. The character is very variable, for any environmental condition that affects these growth factors in one way or the other indirectly increases or decreases the degree of compactness of the terminal part of the rachis.

Before considering the inheritance of the character in squarehead x non-squarehead crosses, it may be well to illustrate the mode of inheri-

TABLE 3. DEGREE OF SQUAREHEADEDNESS IN VULGARE x VULGARE CROSSES

	Generation	Degree of squareheadedness																	Mean	Number of plants
		0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65		
Parent plants																				
Mealy	...	..	..	1	2	6	2	7	4	4	1	1	..	..	..	..	..	..	1.14	28
Jones Longberry	...	..	..	..	1	2	6	3	2	1	..	..	..	..	..	..	..	..	1.12	15
Pride of Genesee	...	..	1	3	4	2	4	6	1	1	1	..	..	..	..	..	..	..	1.08	23
Dawson Golden Chaff	...	2	1	6	6	2	..	..	..	..	..	..	..	..	..	..	..	..	0.98	17
Crosses																				
13158a Mealy x Jones Longberry	F_1	..	..	..	..	..	..	..	..	..	3	1	1	1	..	..	..	..	1.35	6
13158a Mealy x Jones Longberry	F_2	..	..	2	7	13	14	9	5	6	4	1	..	..	..	..	..	..	1.12	61
13178a Jones Longberry x Mealy	F_1									1					2	1	2		1.50	6
13178a Jones Longberry x Mealy	F_2	1	..	3	3	8	9	5	6	4	9	2	3	1	..	..	..	1	1.17	55
13179a Jones Longberry x Mealy	F_1	..	..	..	..	..	..	..	..	..	..	1	..	2	..	..	..	..	1.42	3
13179a Jones Longberry x Mealy	F_2	1	4	3	13	17	15	17	10	4	4	2	..	..	..	..	..	..	1.11	90
13177a Dawson Golden Chaff x Pride of Genesee	F_1	..	..	..	1	1	3	2	..	..	..	..	..	..	..	..	..	..	1.09	7
13177a Dawson Golden Chaff x Pride of Genesee	F_2		1	5	25	14	9	6	6	2	1	1	..	..	..	..	..		1.06	70

tance of squareheadedness when either the squareheads or the *vulgare* type (non-squareheads) are crossed among themselves.

The degree of squareheadedness in F_1 and F_2 generations of *vulgare* x *vulgare* crosses is shown in table 3. The first three crosses here (series 13158a, 13178a, and 13179a) are between Mealy and Jones Longberry, both of which have practically the same degree of squareheadedness, 1.14 and 1.12, respectively. The mean degree of squareheadedness of the F_2 generation fluctuated around the means of their parental forms, being, respectively, 1.12, 1.17, and 1.11.

The fourth cross, 13177a, was made between plants of lower coefficient; that of Pride of Genesee was 1.08 and that of Dawson Golden Chaff was 0.98. The F_2 generation from this cross were all non-squareheads and had a mean squareheadedness of 1.06, these also somewhat approaching the average of their parents.

The degree of squareheadedness in crosses between squareheads is shown in table 4. The F_2 of the first cross, 13201a, has a range with-

TABLE 4. DEGREE OF SQUAREHEADEDNESS IN SQUAREHEAD X SQUAREHEAD CROSSES

	Generation	Degree of squareheadedness																								Mean	Number of plants
		1.0–1.4	1.5–1.9	2.0–2.4	2.5–2.9	3.0–3.4	3.5–3.9	4.0–4.4	4.5–4.9	5.0–5.4	5.5–5.9	6.0–6.4	6.5–6.9	7.0–7.4	7.5–7.9	8.0–8.4	8.5–8.9	9.0–9.4	9.5–9.9	10.0–10.4	10.5–10.9	11.0–11.4		
Parent plants																											
New Soules	..	..	..	..	..	..	..	..	..	2	..	3	..	3	2	2	1	2	..	..	..	..	..	1.71	15
Giant Squarehead	..	..	..	..	..	..	2	..	1	..	3	1	1	5	4	4	1	4	1	3	2	1		1.77	33
Jones Mammoth Amber	..	..	..	..	..	2	..	2	2	2	4	2	..	1	..	..	..	..	..	..	..	..		1.49	15
Crosses																											
13201a New Soules x Giant Squarehead	F_1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	2	1	..	..	..	..	1.87	5
13201a New Soules x Giant Squarehead	F_2	1	..	2	4	4	11	8	12	7	10	2	2	6	1	2	..	..	..	..	..	..	..	1.46	72
13203a Jones Mammoth Amber x Giant Squarehead	F_1	..	..	..	..	..	..	1	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	1.55	3
13203a Jones Mammoth Amber x Giant Squarehead	F_2	..	..	..	2	1	7	4	7	6	4	5	7	3	2	2	..	..	1	..	1	..	..	1.53	52

in the squarehead classes with a mean of 1.46. Compared with the averages of the parental forms—New Soules, 1.71, and Giant Squarehead, 1.77—the mean of the F_2 is lower. The second cross, 13203a, has an F_2 mean squareheadedness within the means of the parents.

There are two points of interest in connection with these two sets of crosses: first, as a rule, when *vulgare* forms are crossed among themselves or squareheads are crossed among themselves, the F_2 generation

TABLE 5. DEGREE OF SQUAREHEADEDNESS IN SQUAREHEAD x VULGARE CROSSES

	Generation	Degree of squareheadedness																																								Mean	Number of plants
		0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3								
Parent plants																																											
Giant Squarehead																	2		1		3	1	1	5	4	4	1	4	1	3	2	1									1.77	33
New Soules																				2		3		3	2	2	1	2														1.71	15
Extra Early Windsor															1		6	3	4	4	1	1	2	1			1															1.57	24
Jones Mammoth Amber														2		2	2	2	4	2			1																			1.49	15
Minnesota 169						1	2	6	8	8	8	5	1	2																											1.15	41
Mealy						1	2	6	2	7	4	4	1	1																											1.14	28
Fultz					1	3	1	3	3	2																															1.04	13
Fultzo-Medit.								5	1	5	2																														1.12	13
Pride of Genesee					1	3	4	2	4	6	1	1	1																												1.08	23
Jones Longberry							1	2	6	3	2	1																													1.12	15
Rural New Yorker							1	6	2	2	1																														1.08	12
Crosses																																											
13131a Giant Squarehead x Minn. 169	F_1													1																											1.35	1
Ditto	F_2						11	11	11	17	21	18	17	4	8	5	3	1	1	4		1	1			1														1.24	135
13150a Minn. 169 x Giant Squarehead	F_1													2		1	1																								1.41	4
Ditto	F_2						3	3	3	5	7	18	9	6	3	5	4	2	1	2	3							1												1.31	75
13156a Minn. 169 x Giant Squarehead	F_1											1		1			2																								1.40	4
Ditto	F_2							4	6	6	9	4	8	8	9	5	2	5	4	1	1	1	1																		1.33	74
13134a Giant Squarehead x Mealy	F_1																		1	1																					1.62	2
Ditto	F_2				1	2	6	4	11	9	7	11	9	8	7	2	2	3	6		4	3																			1.29	95
13135a Giant Squarehead x Mealy	F_1																1		1	2	1																				1.62	5
Ditto	F_2			1	2	1	2	6	1	7	11	11	11	12	9	11	12	8	5	2	4		1	2	1	1															1.36	121
13137a Giant Squarehead x Fultz	F_1															1	1		1																						1.51	3
Ditto	F_2	1			4	8	14	13	9	8	11	6	5	7	4	4	3	6	2	2	1			2	1																1.21	111
13138a Fultz x Giant Squarehead	F_1												1		1		1	1	1																						1.47	5
Ditto	F_2		1		1	2	8	13	11	4	8	7	7	8	3	6	1	1	1	2	1	4																			1.22	89
13140a Giant Squarehead x Fultzo-Mediterranean	F_1																						1	1																		1.77	2
Ditto	F_2						1	2	3	3	6	10	8	14	12	10	9	7	7	4	1	2	1							1											1.40	101
13141a Giant Sq. x Pride of Genesee	F_1															1		1		1																						1.55	3
Ditto	F_2						4	8	10	10	6	13	5	1	7	2	2	1	1			1																				1.22	71
13200a Pride of Genesee x Giant Squarehead	F_1	Not recorded																																									
Ditto	F_2		1		1		3	7	5	7	8	10	7	6	3	6	4		3		1	1	2		1																1.28	76
13202a Jones Longberry x Giant Sq.	F_1																			2	2																					1.68	4
Ditto	F_2					1	4	4	6	2	9	8	6	7	12	4	2	2	4	1	1		1																		1.30	74
13194a Pride of Genesee x New Soules	F_1															3		1	1	1																						1.52	6
Ditto	F_2						4	3	6	9	10	11	4	7	3	2	1	4		1																						1.24	65
13144a New Soules x Pride of Genesee	F_1																					1																				1.75	1
Ditto	F_2					1	6	10	4	9	5	13	3	4	3	10	2	1	2	1	1			1																	1.25	76
13176a New Soules x Rural New Yorker	F_1													2			1																								1.40	3
Ditto	F_2			1			4	4	13	5	13	9	11	7	7	3	5	1	2																						1.25	85
13196a Pride of Genesee x Extra Early Windsor	F_1													2			1	1																							1.46	4
Ditto	F_2						3	2	6	8	14	11	12	10	6			1																							1.24	73
13193a Jones Mammoth Amber x Mealy	F_1														1	1																									1.42	2
Ditto	F_2					3	4	13	14	14	9	7	8	7	3	4	3	2	2	1		1																			1.22	95
13143a Extra Early Windsor x Pride of Genesee	F_1	Not recorded																																									
Ditto	F_2						1	4	3	10	7	12	8	4	5	5	2		1	1	1																				1.27	64

consists of practically only *vulgare* or only squareheads, respectively; secondly, the mean of the F_2 generation approaches the average of the parental forms.

Regarding the inheritance of squareheadedness among squarehead x *vulgare* crosses, an idea can be obtained by comparing the F_2-generation distributions with the parental distribution (table 5). Special attention might be called to the comparatively high degree of squareheadedness of the F_1 generations; in most of the cases the F_1 plants are almost as squareheaded as the squarehead parents. On a theoretical basis the means of the F_1 would be expected to coincide with those of the F_2. The departure here is too wide. This increase in squareheadedness of the F_2 is attributed both to heterosis and to greater care taken in growing and spacing the plants of this generation.

The F_2-generation distribution, even when the number of individuals of which they are composed is considered, shows certain characteristics with respect to range of distribution and mean. If the F_2 distributions of squarehead and non-squarehead crosses are compared with those of the crosses in which the parents were either both squareheads or both *vulgare*, it is seen that so far as the mode of inheritance is concerned there is no essential difference between them. The means of the F_2-generation plants shift toward or away from the more squarehead classes, but show a constant tendency to regress toward the means of the parental forms; and the range of the F_2 also spreads or contracts, depending on the extent to which the parents vary in degree of squareheadedness.

Although several of these crosses were carried through the F_3 generation because of the similarities of the results, only two series are considered here to illustrate the behavior of the F_2 plants in F_3. The results of Giant Squarehead x Fultzo-Mediterranean (series 13140a) are shown in table 6, and those of Giant Squarehead x Mealy (series 13135a) are shown in table 7.

TABLE 6. BEHAVIOR OF SQUAREHEADEDNESS OF F_2 PLANTS IN F_3, SERIES 13140a, GIANT SQUAREHEAD × FULTZO-MEDITERRANEAN

		Degree of squareheadedness																													Mean	Number of plants
		0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15	2.20				
P_1 Giant Squarehead		.				.					2		1		3	3	1	5	4	4	1	4	1	3	2	1					1.77	33
P_1 Fultzo-Mediterranean		.			5	1	4	3																							1.12	13
F_1		.																	1	1											1.77	2
F_2		.		1	2	3	3	6	10	8	14	12	10	9	7	7	4	1	2	1				1							1.40	101
F_3 families																																
Pedigree	Squareheadedness in F_2																															
24-1	1.36	1	1	3	6	4	7	4	3	3	3	1	.	1																	1.16	37
24-2	1.61	.	.	1	3	2	4	4	3	4	5	1	3				1	1													1.27	32
24-3	1.33	.	.	1	6		4	5	2	3	1		.																		1.17	23
24-4	1.28	.	.	2	3	1	2	12	12	2	3	3	2																		1.23	42
24-5	1.54	.	.	.	1	1	2	3	2	4	3	4	2		1		1		1												1.33	25
24-6	1.62	.	.	1	3	2	9	2	6	7	1	3	.	1																	1.22	35
24-7	1.51	.	.	1	2	2	4	6	1	2	1	1	1	3					1												1.30	25
24-8	1.17	1	1	3	6	9	5	1	4	.						.															1.10	30
24-9	1.59	.	.	.	1	1	1	2	4	1	1	2	4	2	2	1	1		1												1.38	24
24-10	1.45	.	.	2	2	2	2	3	6	6	4	6	2	3	2	3					1										1.33	44
24-11	1.34	.	.	1	3	2	10	6	3	1	2		1			.															1.18	29
24-12	1.64	.	.	1	.	1	1	.	3	3	5	2	4	3	4	1	3	5	2					1							1.47	39
25-1	1.36	.	.	2	3	4	4	4	4	4	1		3						1												1.22	30
25-2	1.37	1			1	2	2		1			2								1											1.23	10
25-3	1.01	1	6	14	7	8		2		1																					1.04	39
25-4	1.21	2	1	6	8	9	3	1																						.	1.05	30
25-7	1.52	.	.	.	2	3	5	3	10	8	1	2	1	5																	1.27	40
26-1	1.28	.	.	1	3	3	4	6	5	4	4	4	2	1																	1.25	37
26-2	1.37	.	.	1	. .	3	4	6	4	3	1	9	4	4	5	2															1.34	43
26-3	1.42	.	.	.	. .		2	1	1	1	2	2	1	2	1	2	2	1													1.43	18
26-4	1.40	.	1	.	. .		1	5		6	5	4	1	2	2	3	1		1	1											1.39	33
26-5	1.50	.	.	1	. .	3	1	1		4	3	2	1	1	4	1	4	1		1											1.42	28
26-6	1.52	.	.	.	5	.	9	4	9	8	3	1		1																	1.22	43
26-10	1.48	.	1	1	1	3	8	4	2	2	2	1	2	1	1																1.22	29
26-11	1.57	.		1	7	2	7	4	5	2	1	1	2	1																..	1.19	33
26-12	1.45	.		1	1	1	2		3	9	2	2	5	3	2	3			1												1.35	39
26-13	1.20	.			. .	1	3	2	6	1	5	3	3	1	2				2												1.35	29
26-14	1.50	.			1	2		5	3	4	5	5	3	7	4	1	2	1	1	2										1	1.44	45

Total number of F_3 plants..... 911

TABLE 7. BEHAVIOR OF SQUAREHEADEDNESS OF F_2 PLANTS IN F_3 SERIES 13135a, GIANT SQUAREHEAD × MEALY

		Degree of squareheadedness																													Mean	Number of plants
		0.87	0.90	0.97	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10		
P_1 Giant Squarehead		..	.	..	..	..	..	..	..	..	..	2	..	1	..	3	1	1	5	4	4	1	4	1	3	2	1	1.77	33
P_1 Mealy				1	2	6	2	7	4	4	1	1																1.14	28
F_1		..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	2	1										1.62	5
F_2		1	2	1	2	6	1	7	11	11	11	12	9	11	12	8	5	2	4		1	2	1	1				1.36	121
F_3 families																													
Pedigree	Squareheadedness in F_2																												
19-6	1.22			3	9	12	5	7	1	1	1	.		.														1.07	39
19-16	1.23		1	3	5	6	4	2		.	1	..																1.05	22
20-2	1.26				1	1	2	3	1	2	2	5																1.22	17
18-2	1.26						1	1	2	2	2	3	1	2	2		2											1.35	18
19-5	1.28		1		1	1	5	10	3	5	1																	1.15	27
20-4	1.31			1	1	4	3	6		4	.	2	2															1.17	23
19-17	1.32			1	3	3	6	8	2	5	3	2																1.16	33
19-12	1.33					2	.	1	1	4	2	8	3	4	3	2				1								1.36	31
19-2	1.39		1		1	7	14	9	1	5	1	1			1					1	1				1			1.18	44
20-10	1.39					1	1	3	7		3	2	1	1	1	1												1.25	21
19-9	1.40					1	.	3	3	1	.		1															1.19	9
19-11	1.42					1	3	4	3	5	8	6	2	3		.			1		1						.	1.30	38
19-7	1.44			1			1	2	2	4	4	3	2		.													1.26	20
18-1	1.45			1			.	1	6	6	5	5	1	..	1		1											1.28	27
20-5	1.46	1	1				1	2	4	.	1	1	3	1	..	.	1		1									1.26	20
19-3	1.47				1	1		5	4	4	8	6	1	5	5	2	2			1								1.34	45
19-8	1.47			1		5	6	8	5	6	3	1		..	..													1.16	35
20-8	1.47				1	2		4	3	3	2	4		1	2	.												1.25	22
19-14	1.48			1		1	7	5	1	4		2		..	1	1											..	1.20	21
20-3	1.49					1	1	1	4	2	2	1	3	..	..	1	1											1.29	17
19-4	1.50							1	3	3	2	2	3	1	3	1		1	1									1.37	21
19-18	1.50					.				1	2	8	6	4	4	2	2			1								1.43	30
20-9	1.50		1		1	4	1	7	7	5	2	1	4	1	1	..	..											1.21	35
19-15	1.51			..			.	2	6	3	6	4	4	1	2	1	1		1									1.33	31
19-20	1.52						1		2	5	2	7	3	..	2	1	1	1	1									1.26	29
20-1	1.54					1	3	3	5	4	5	2	3	1	1		..	..										1.25	29
20-12	1.54		1	1	4	5	3	6	7	3	2	3		..	..		..	..										1.15	35
20-5	1.55		1				..	1	2	2	4	1	3	1	4		..	1					..					1.34	20
18-3	1.55			1	2	5	3	8	7	7	6	..	..	.			.				.							1.18	39
20-13	1.56			2	1	1	4	6	1	4	1	2	4	3	1	1					.							1.24	31
19-19	1.57			1		1	2	4	2	3	2	2	1	1	1	.	1				.							1.25	21
20-7	1.59						1		2	5	2	7	3	.	2	1	1	1	1		.							1.36	26
19-13	1.64						2	1	3	6	5	9	2	3	.	2	..	1	.	1					1			1.35	36
19-1	1.72				2		3	8	7	7	8	10	6	6	2	.	..	1			.							1.29	60
20-11	1.74			1	1	1	2	4		2	2	4	1	..	1	1	2	1	2	..	..	..	..	..	..	..	..	1.32	25
19-10	1.88				1	2	6	6	6	3		3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.18	28

Total number of F_3 plants 1,022

That a segregation of forms is taking place is quite evident. The F_3 distributions shown in table 6 are arranged in the order in which they were planted, so that the differences may not be ascribed to environmental conditions. Cultures 24-8, 25-3, and 25-4 show notable differences in distribution and mean from the cultures growing next to them. Similarly, in table 7, where the F_3 distributions are arranged according to the degree of squareheadedness of the F_2 plants, the difference in squareheadedness of cultures 19-17, 19-18, and 19-19, and many others, is to be noted. The progeny of plant 19-17, representing a line in which none of the plants were squareheads, grew immediately next to a row, 19-18, which produced only squareheads, thirty in all.

In order to show that the variations noted in the F_3 are not chance variations but are hereditary, the curves shown in figure 78 were plotted,

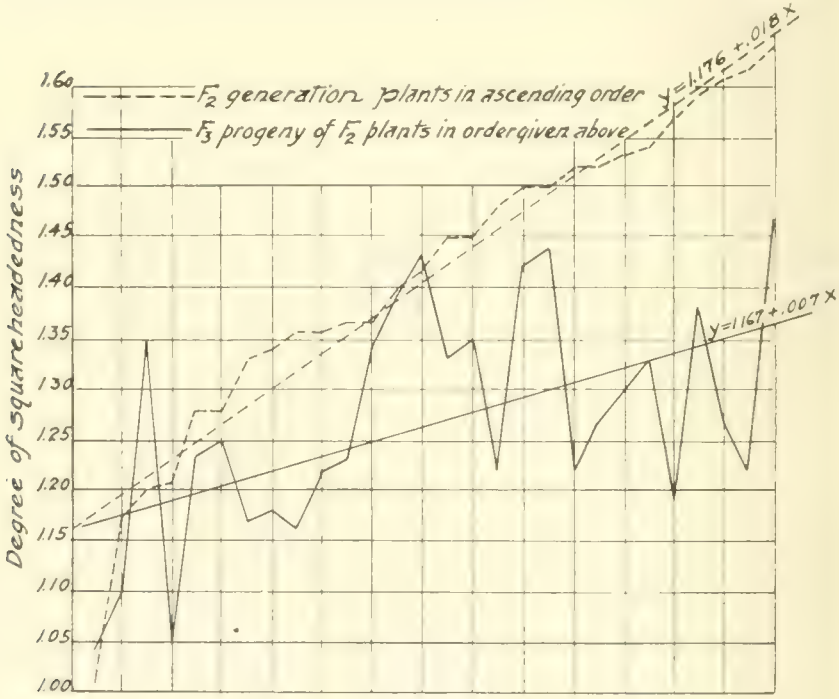

FIG. 78. RELATION OF DEGREE OF SQUAREHEADEDNESS BETWEEN F2 PARENT PLANTS AND THEIR PROGENY

based on the F_3 data of series 13140a (table 6). Two sets of curves are shown in this figure. The dotted curve represents the degree of squareheadedness of the F_2 plants, and the solid curve represents the means of the F_3 in the order of squareheadedness of the F_2 plants.

The inclination of the straight line fitted to the curve of the F_3 progeny shows that in a general way the degree of squareheadedness of the progeny is determined by the degree of squareheadedness of the F_2 parent plants. A few words of explanation may be given to account for the constant rise and fall of this curve. Since the F_3 figures represent, respectively, the means of approximately thirty individuals, there is no question that they are dependable, and the differences between the means of the F_3 plants show their comparative genotypic differences. Since the mean of the F_3 in material having a mode of inheritance such as this character fluctuates more or less around the degree of squareheadedness of the F_2 form planted, it may be assumed that, had the F_2 plants been grown in the same year as and under conditions similar to those under which the F_3 were grown, the average degree of squareheadedness of the developed heads of the F_2 planted would have approached more nearly the mean of their progeny. Because of the large number of plants that had to be measured, it was not found practicable to measure several heads from each F_2 plant. A developed head was taken at random from each of the envelopes containing the heads of each plant, and was measured. Since different heads in a single plant vary greatly in squareheadedness, the developed head selected at random does not necessarily show the true phenotype. Therefore, the zigzag nature of the F_3 curve should not be ascribed to inconsistent variations, but to inability to ascertain the true degree of squareheadedness of the F_2 by a single measurement, or even more, of the heads of a single plant.

The difference between the slope of the straight line of the F_2 curve and that of the F_3 is due to two conditions. In the first place, while the F_2 curve represents individual plants of a single frequency distribution, the F_3 curve represents the means of such distributions. In the second place, as the mean represents the average of all plants exhibiting variations, slight or extreme in either direction, the means of the F_3 cannot vary as much as the individuals of the F_2 in which the extremes

of the frequency distribution are also included. The slope of the fitted straight line of the F_3 means could therefore not be expected to be as steep as that of the F_2-generation plants.

Squareheadedness is not peculiar to the lax form commonly known as *squarehead.* It may be present or absent in other forms also. The *compactum* forms usually are squareheaded but there are also many which are not. In the examples that follow it is shown that squareheadedness introduced by a club has the same effect on the forms of the succeeding generations as does squareheadedness introduced by the ordinary lax squarehead.

The dense squarehead of the compacto-capitatum form used in this study was that known as *Dale Gloria* (Plate LXVII, upper, 5). This form is very dense and has an average internode length varying usually from 1.2 to 1.7 millimeters. Its degree of squareheadedness ranges from low to high, as shown in table 8. With very dense wheats such as Dale

TABLE 8. INHERITANCE OF SQUAREHEADEDNESS IN A SQUAREHEAD x COMPACTUM CROSS
(Series 13173a, Dale Gloria x New Soules)

	Degree of squareheadedness																				Mean	Number of plants
	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90		
Dale Gloria	1	1	1	2	1	..	4	1	..	2	..	2	..	..	1	1	..	..	..	..	1.28	17
New Soules	..	..	..	..	..	..	..	..	..	..	..	2	..	3	..	3	2	2	1	2	1.71	15
13173a F_1	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	2	..	..	..	1.65	4
13173a F_2	..	..	..	4	..	1	2	3	5	5	4	3	1	3	2	1	3	2	2	..	1.46	41

Gloria, there is a certain limit beyond which the internodes do not shorten further. This is particularly true when the terminal spikelets are fertile, for development of a spikelet and development of adjacent parts—glumes, nodes, internodes—seem to go hand in hand. A slight increase in the length of the terminal internodes of heads having an internode length in this region as short as 0.8 to 1.2 millimeters, greatly lowers the degree of squareheadedness. This accounts for the presence of forms of a low degree of squareheadedness among Dale Gloria plants.

In a cross between Dale Gloria and New Soules (series 13173a, table 8), in which both parents were squareheaded, the F_2 plants were found to be practically all in the squarehead classes. There were a few in the non-squarehead classes but these were all dense forms like Dale Gloria.

In a cross such as this, there is also an independent segregation of density in the F_2 generation. Half of these F_2 plants were carried through F_3. The F_3 forms were practically all squareheaded. In some cases there were a few non-squareheads but these were in a very low proportion and probably were genotypically squareheads. As far as squareheadedness is concerned, the Dale Gloria x New Soules cross behaved like any squarehead x squarehead cross, such as those shown in table 4 (page 815).

When Dale Gloria is crossed with *vulgare* forms (table 9), the distri-

TABLE 9. INHERITANCE OF SQUAREHEADEDNESS IN VULGARE x COMPACTUM CROSSES

(13214a, Turkey x Dale Gloria; 1337a, Turkish Amber x Dale Gloria; 13172a, Mealy x Dale Gloria)

	Degree of squareheadedness																					Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80		
Parent plants																							
Dale Gloria	..	..	..	1	1	1	2	1	..	4	1	..	2	..	2	..	..	1	1	..	..	1.28	17
Turkey	2	3	2	2	1	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.92	13
Turkish Amber	1	..	..	3	6	10	6	4	4	..	..	..	..	..	..	..	..	..	..	..	..	1.04	34
Mealy				1	2	6	2	7	4	4	1	1	..	..	..	..	..	..	..	..	..	1.14	28
F_2 plants																							
13214a											..	..	1	..	..	..	1						
1337a	..	..	..	..	..	..	..	..	..	..	..	1	..										
13172a	..	..	..	..	Not recorded				..	..	..	..	..	..	..	..	..	..	..	..	..		
F_3 plants																							
13214a	1	..	5	4	11	10	2	5	9	3	6	3	1	3	2	..	..	..	..	..	..	1.12	65
1337a	..	..	2	1	5	6	7	5	3	9	3	6	4	3	4	2	2	..	1	..	1	1.25	64
13172a	..	1	2	..	2	6	3	3	10	8	6	5	8	5	4	6	4	1	..	2	..	1.31	76

butions of both the F_1 and F_2 generations show a marked resemblance to those produced by squarehead x *vulgare* crosses as shown in table 5 (page 816). The curves of the F_2 in both instances range from the *vulgare* to the squarehead classes. In this case also Dale Gloria behaved as a squarehead; and it is in reality a squarehead, but in addition it happens to carry a density factor.

Two of the crosses in table 9 were carried through F_3. The results were similar to those already observed in tables 6 and 7 (pages 818 and 819). Using class 1.30 as an arbitrary line dividing non-squareheads from squareheads, different F_2 progenies produced non-squareheads and squareheads in different proportions and degrees. There were progenies which consisted of nothing but squareheads, and others which consisted only of non-squareheads.

The question of the inheritance of squareheadedness, and especially that of the relationship of squareheadedness to certain other characters, is considered further in the discussion of inheritance of density. The general facts observed thus far regarding the inheritance of squareheadedness among forms of the *sativum* group may be summarized as follows:

Squareheadedness is not a unit character, but is a resultant of a combination of growth characters which produce shortening of the terminal internodes. The F_2 and subsequent generations show segregation of plants or lines of squareheadedness distinctly varying in degree, but no definite ratios are observed among these. The average degree of squareheadedness of the F_1-generation plants is usually much higher than the mean of the F_2; in some instances in this study it approached that of the squarehead parent. Apparent vigor due to heterosis, and the greater care usually given to F_1 plants, are considered to account for their variation.

Squareheads crossed among themselves or *sativums* crossed among themselves produce, generally speaking, only squareheads or *sativums*, as the case may be, of ranges and means approaching those of the parental forms. The crosses between squareheads and *sativums* show a wide range of variation, but the range and the mean of the F_2 are still determined by those of the parental forms.

Some of the clubs are squareheaded, and these behave as squareheads when crossed with other forms.

RELATION OF THE DEGREE OF SQUAREHEADEDNESS OF THE VULGARE PARENT IN VULGARE X SQUAREHEAD CROSSES, TO THE SQUAREHEADEDNESS OF THEIR PROGENY

The question as to the extent to which the parent plants influence the squareheadedness of their offspring may be determined by examining crosses in which one of the parents is the same in all crosses while for the other parent different forms are used. In table 5 (page 810) a number of series are shown in which different varieties of *vulgare* are crossed with Giant Squarehead. The F_1 and F_2 generations of these crosses are shown graphically in figure 79, in which the crosses are arranged according to the degree of squareheadedness of the *vulgare* parent.

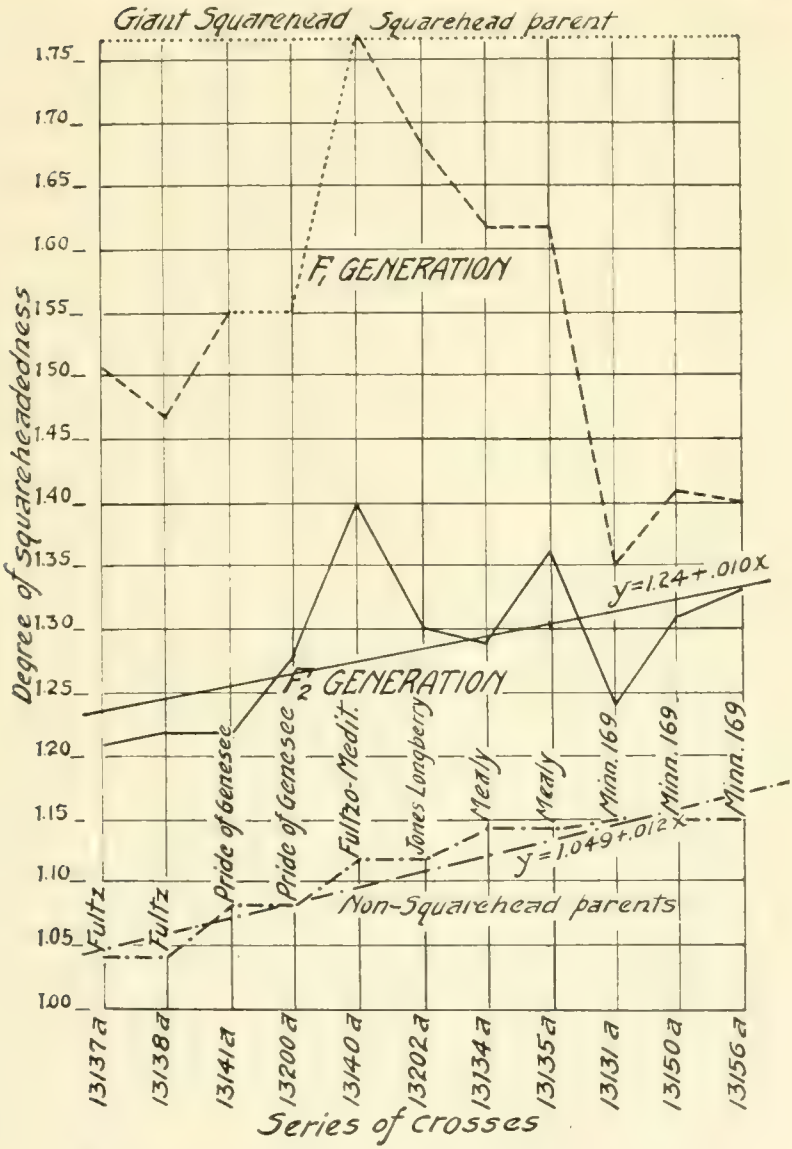

FIG. 79. DEGREE OF SQUAREHEADEDNESS OF PARENTS AND PROGENY WHEN DIFFERENT VULGARE FORMS WERE CROSSED WITH GIANT SQUAREHEAD

The curves representing the means of both the F_1 and F_2 generations show intermediacy between the parental curves. The F_1 curve, as has already been mentioned, shows, as a rule, a higher degree of squareheadedness than the F_2. The F_2 curve shows a general rise of the mean more or less in proportion to that of the *vulgare* parental curve. The F_1 curve, being based on measurements of very few plants, shows great irregularities although it follows the general lines of the F_2 curve.

The curve to be considered is that formed by the F_2 means. Although this curve shows a general rise, it cannot be said that the means of the F_2 increase or decrease directly in proportion with the means of the *vulgare* parents. There are other factors introduced by the *vulgare* parents which, combined with those contributed by the squarehead parent, tend to neutralize or accelerate the production of squareheadedness. For example, Fultzo-Mediterranean produced an F_2 progeny of a very high degree of squareheadedness, and the corresponding rise of the F_1 curve shows that this rise is significant. Mealy and Minnesota 169, although of a higher degree of squareheadedness, produced individuals of lower mean squareheadedness.

The influence of the *vulgare* parent on the squareheadedness of *vulgare* x squarehead-compact crosses is seen in table 9. In the crosses in this table the squarehead-compact parent is Dale Gloria. The *vulgare* parents, Turkey, Turkish Amber, and Mealy, have coefficients of 0.92, 1.04, and 1.14, respectively. The ranking of the F_2 means is in the same order, and coincidently the differences between them are in proportion with the differences existing between the *vulgare* parents.

Because crosses between squareheads produced only squareheads, and those between *vulgare* forms only *vulgare* forms, it cannot be concluded that the degree of squareheadedness of the offspring is entirely dependent on that of the parents, for the determining factor is not the degree of squareheadedness of the parental forms but the peculiar combination of factors introduced by each variety. The mean squareheadedness expressed by a variety is but the resultant of the effects of these factors.

FALSE DOMINANCE OF SQUAREHEADEDNESS

Since the F_2 progeny of a *vulgare* x *vulgare* cross consists only of *vulgare* forms, theoretically one would expect such a cross to produce

only non-squareheads in F_1. This has not always been the case. In table 3 (page 814), giving the results of three Mealy x Jones Longberry crosses, the parental means are 1.14 and 1.12, averaging 1.13, and the means of the F_2-generation plants are 1.12, 1.17, and 1.11, also averaging 1.13. But the F_1-generation plants in all three cases were distinctly squareheads, with means of 1.35, 1.50, and 1.42, respectively. In this paper the figures for squareheadedness or for density of F_1 plants represent the averages of usually from five to ten heads of each plant. If the apparent degree of squareheadedness of the F_1 plants indicated their approximate genotypic make-up, it would be expected that the F_2 distribution would range somewhat near the mean of the F_1 plants. The F_2 plants in these three cases were all *vulgare*, showing that the appearance of F_1 plants of a high degree of squareheadedness in these cases did not show any type of dominance of squareheadedness.

These crosses may be contrasted with the Dawson Golden Chaff x Pride of Genesee cross (13177a), in which the F_1 plants were all *vulgare*, their mean approaching that of the F_2.

The appearance of squareheads in the F_1 generations of series 13158a, 13178a, and 13179a, and the absence of such forms in 13177a, may be accounted for by the supposition that in the first three crosses the combinations of growth factors contributed by the parents were favorable to the production of squareheads, while those contributed by the parents in series 13177a were not favorable.

The presence of squareheads in F_1 and their total absence in F_2 in series 13158a, 13178a, and 13179a, may be regarded as cases of false dominance.

RELATION OF WIDTH OF CULM TO SQUAREHEADEDNESS

The part of the culm below the base of the spike tends to be wider in squareheads than in heads of uniform internode length. The data here considered were taken on the progeny of a lax squarehead x *vulgare* cross, which was not as favorable a material for the study of this character as would have been some other crosses in which a more intense squarehead was used. The results, however, were satisfactory enough to illustrate the degree of correlation between squareheadedness and width of culm.

In taking measurements for squareheadedness of the F_3 generation of series 13135a, the width of the culms of some 260 heads was measured also. The measurement was taken about 2 centimeters below the basal rachis internode. The resulting data are shown in correlation form in table 10. The coefficient of correlation in this distribution is 0.465 ± 0.033, which is significant.

TABLE 10. CORRELATION BETWEEN DIAMETER OF CULM AND SQUAREHEADEDNESS (Series 13135a, Giant Squarehead × Mealy)

Diameter of culm (millimeters)	Degree of squareheadedness 0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
1.4			1							
1.6			1							
1.8	1	4	9	10	3	1		1		
2.0	1	11	25	28	12	8	1			
2.2		2	15	18	8	5	4	4		
2.4		3	7	12	15	13	5	2	1	
2.6			1	2	6	7	6	2		1
2.8					3	1	2			

$r = 0.465 \pm 0.033$

The writer considers this correlation as not due to any form of linkage but as a direct result of squareheadedness, which is caused in turn by the shortening, or rather hampering of the development, of the terminal part of the spike due to pressure produced by rapid development of the culm internode immediately at the base of the head, and to the failure of the sheath enveloping the spike to grow at a corresponding rate. When the longitudinal growth of the culm internode is checked or retarded, growth naturally takes place in other directions, often causing a thickening of the culm wall. A similar thickening of the wall of the culm occurs also in non-squarehead dense plants and more pronouncedly in squarehead dense plants. In these cases, however, the thickening seems to be due to the presence of the density factor, which shortens the culm internode length as well as the length of the rachis internode. Due to dwarfing, the plant cannot grow in height. The food produced constantly by the plant is stored partly in the culm, thus increasing the thickness of its walls.

The club wheat owes its ability to stand erect in the presence of strong winds to the presence of the density factor, which, as mentioned above, produces thickening of the culm and incidentally of other parts. This factor, which is later considered at length, causes the shortening of the culm also, without affecting the number of nodes. The shortening of the culm internodes increases the number of nodes to each unit of length, thereby giving the culm added strength; moreover, the shortening of the culm lowers the leverage. These three conditions, direct or indirect results of the presence of the density factor, are the chief causes of the non-lodging quality of dense wheat.

INHERITANCE OF SQUAREHEADEDNESS IN SPELT X SATIVUM CROSSES

In crosses wherein the spelt character has been introduced, the curve of the F_2 generation is very distinctly skewed near the extreme of the range on the side of the non-squarehead classes (table 11). True spelts

TABLE 11. SQUAREHEADEDNESS IN SPELT X SATIVUM CROSSES

	Degree of squareheadedness																													Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15	2.20		
13125a Crimean x White Spelt..						No squareheads																									
13260a White Spelt x Turkey.						No squareheads																									
13216a Giant Squarehead x White Spelt ...	3	12	12	11	14	5	3	2	1	1	2	..	2	3	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1.01	73
13255a White Spelt x Dale Gloria	5	7	10	2	11	4	6	4	2	..	7	3	2	1	1	2	2	1	..	1	..	..	..	..	..	..	..	..	..	1.10	71
3085a Black Bearded Spelt x Jones Longberry..........	..	..	..	4	17	4	6	3	2	1	..	1	..	..	1	2	..	..	2	1	..	..	1	..	2	1	1	..	1	1.24	50

differ in their ability to carry the factors producing squareheadedness. It cannot be determined from the appearance of the spelt plants whether or not they carry the squareheading factors, as the spelt character acts as an inhibitor for squareheadedness. In fact, the presence of a large number of individuals in the non-squarehead classes of spelt x *sativum* crosses is the result of the presence of a large number of spelts, which, although carrying the squareheadedness factors, were themselves non-

squareheads because they carried also the spelt factor, which, as stated above, acts as an inhibitor for the squarehead character.

Five crosses between spelts and *sativums* are shown in table 11.[5] Series 13125a and 13260a, which were crosses between *vulgare* and White Spelt, produced F_2 generations composed of non-squareheads only. When this same spelt form was crossed with Giant Squarehead (series 13216a), a number of squareheads were produced in F_2. The White Spelt x Dale Gloria cross (13255a) also showed a fair number of squareheads (Plate LXVII, upper, 6 to 12).

From these results it is seen that the White Spelt does not carry the necessary factors for squareheadedness, since when it was crossed with *vulgare* it produced no squareheads. Squareheads appeared only when a squarehead form was used as the *sativum* parent.

These four crosses were carried through F_3. The first two crosses produced practically no squareheads; a few were obtained, but they were not tested to ascertain their stability. The remaining crosses produced F_3 progeny which were composed of forms of various degrees of squareheadedness. Since the spelt factor acted as an inhibitor, the spelts of the F_3 showed no squareheadedness. The non-spelts produced curves similar to those shown in tables 6 and 7.

That there was no so-called repulsion between the spelt and squareheadedness factors was evident from the reappearance of squareheads among the progeny of some F_2 spelts, and from the absence of squareheads among the offspring of other F_2 spelts.

Another spelt form, known as Black Bearded Spelt, when crossed with a *vulgare*, Jones Longberry (series 3085a), produced a large number of squareheads. These forms were more intensely squareheaded than those produced by the White Spelt x Giant Squarehead cross (13216a).

About ten spelt x *vulgare* crosses, with Black Bearded Spelt as one of the parents, were examined by the writer, and in every case there were a large number of squareheads in the progeny, most of which were semi-dense.

The progeny of cross 3085a were not carried through F_2, but another

[5] The F_2 segregations of these crosses were in the proportion of 3 spelts or spelt-like forms to 1 *sativum*.

cross between this same Black Bearded Spelt and a *vulgare* showed that most of the squareheads bred true.

If it is recalled that some of the F_2 spelts of the squarehead x White Spelt cross produced squareheads in F_3 while others that were phenotypically like the former did not, it will not be difficult to understand how the Black Bearded Spelt could have produced different results from those of the White Spelt. It appears, from these examples, that spelts may carry the squareheadedness factors the same as do squarehead *sativums* themselves, but due to the presence of the spelt factor, which acts as an inhibitor, such spelts do not appear squareheaded.

This leads to the consideration of another condition. Since the presence of squareheadedness cannot be detected without a genetic analysis, one may come across a spelt form which, crossed with *vulgare*, may sometimes yield squareheads and sometimes not. Either such a spelt is heterozygous with respect to squareheadedness, or the variety to which it belongs has not been stabilized with respect to this character. As the investigator is guided by apparent characters in purifying a line or in calling it a pure line, he cannot detect the segregation of non-detectable factors which is going on within his selected line.

EFFECT OF THE SPELT FACTOR ON SQUAREHEADEDNESS

In the discussion of the inheritance of squareheadedness in spelt x *sativum* crosses, it was mentioned that the spelt factor inhibited square-

TABLE 12. RELATION OF SQUAREHEADEDNESS TO SPELTING
(Series 13216a, Giant Squarehead x White Spelt)

Degree of spelting	Degree of squareheadedness: 0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55
1	1	3	3	3	2											
2	1	2	1	1		2										
3	1		1	1	2	2										
4		1	3	1	1											
5		2	2	1	3		1									
6		1	1	3	2											
7		1			1			1								
8		2		1	2					1						
9			1		1	1	2	1	1		1		2	1		1
10											2			2		

TABLE 13. RELATION OF SQUAREHEADEDNESS TO SPELTING

(Series 13255a, White Spelt x Dale Gloria)

Degree of spelting	Degree of squareheadedness																			
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75
1	3	3	6	2		1			1											
2	2	1	3		2		2													
3		1	1		3		2	1			1									
4					1	1	2													
5		2			1	1		1												
6												1								
7					1			1			2									
8																				
9															1	1				
10					3	1		1	1		4	2	2	1		1	2	1		1

TABLE 14. RELATION OF SQUAREHEADEDNESS TO SPELTING

(Series 3085a, Black Bearded Spelt x Jones Longberry)

Degree of spelting	Degree of squareheadedness																					
	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.00 +
1	2	5	1		1																		
2	1	2	2	2	1																		
3		4																					
4		1			1																		
5		2		2																			
6																							
7		3		1																			
8						2																	
9							1		1													1	
10	1		1	1							1	2				2	1			1		1	3

headedness. The object here is to show to what extent this inhibition takes place. To illustrate this, three types of crosses are used. The first is the Giant Squarehead x White Spelt cross (table 12); the second is White Spelt x Dale Gloria (table 13); and the third is Black Bearded Spelt x Jones Longberry (table 14). In the first two crosses, squareheadedness is introduced by a lax squarehead and a dense squarehead, respectively, and in the last cross it is introduced by the spelt.

The F_2 plants in these tables are classified into ten arbitrary classes of spelting. The spelts in such crosses exhibit the spelt character in various degrees. Those showing it in an intense form are placed in class 1; classes 2, 3, 4, and so on up to 9, show various degrees of dilution of the character; the plants in class 10 are all *sativum* forms, and lack the spelt altogether.[6]

The distribution of the plants with respect to spelting and squareheadedness, as shown in tables 12 to 14, seems to depend to a great extent on the types used as parents. Different spelts crossed with different *sativums* show different modifications. All crosses, however, show the following general distribution: Spelts of classes 1 to 5 inclusive arrange themselves more or less within the non-squarehead classes 0.80 to 1.15. There is a slight tendency in spelt classes 3 to 5 to move the mean toward 1.15. As the classes approach the *sativum* type, the shifting of the mean toward the more squareheaded classes is accelerated in geometrical proportion.

The spelt factor, then, does not prevent squareheadedness altogether, but plants that are heterozygous spelts or those that carry modifiers tending to dilute this spelt character are very much more likely to be squareheaded than plants that are intensely spelted. Squareheadedness in spelts, however, is always of a low degree.

INHERITANCE OF SQUAREHEADEDNESS IN SPECIFIC CROSSES

It has already been shown (page 829) that when Black Bearded Spelt is crossed with a *sativum* of a uniform rachis internode length, an appreciable number of squareheaded forms appear in the F_2. Squareheads may be obtained also when a *vulgare* is crossed with other species. In table 15 the progeny of a number of interspecific crosses are classified into two groups, the first containing forms resembling the *sativum* type and the second including all the other forms. Their degree of squareheadedness is represented in the usual manner.

In all series a large proportion of the *sativum* or *sativum*-like forms were squareheads. The segregates belonging to other species were practically all non-squareheads.

[6]The genetics of the spelt character with reference to the crosses under consideration has been fully discussed in a recent paper (Leighty and Boshnakian, 1921).

TABLE 15. DEGREE OF SQUAREHEADEDNESS IN SPECIES CROSSES. F_2 DATA

3032 Salt Lake Club x Kahle (*Triticum durum*)
3034 Gharnovka (*T. durum*) x Black Bearded Spelt (*T. spelta*)
1312a Poole (*T. vulgare*) x Alaska (*T. turgidum*)
1328a Satisfaction (*T. vulgare*) x Alaska (*T. turgidum*)
1360a Jones Paris Prize (*T. vulgare*) x Kubanka (*T. durum*)

F_2 generation results	Degree of squareheadedness																									Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00†		
3032—																											
Sativum and *sativum*-like forms	..	..	..	4	..	2	2	..	2	1	4	6	5	1	2	2	..	2	..	2	..	..	..	..	..	1.32	35
All other forms	..	..	1	3	2	1	1	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.04	11
3034—																											
Sativum-like forms *	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	1	..	..	..	2	1.81	5
All other forms	..	..	2	7	24	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.99	36
1312a—																											
Sativum and *sativum*-like forms	..	..	..	2	1	2	..	2	4	2	1	..	2	..	1	..	..	..	1	..	..	2	..	..	2	1.38	22
All other forms	..	4	13	8	13	8	4	1	2	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	1	1.08	58
1328a—																											
Sativum and *sativum*-like forms	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	4	1.69	8
All other forms	3	3	5	4	7	5	1	5	2	1	2	1	..	..	1	..	..	..	1	..	..	..	..	..	..	1.10	41
1360a—																											
Sativum and *sativum*-like forms	..	..	..	..	..	1	1	..	..	3	..	..	..	2	1	..	..	1	..	..	..	..	..	..	..	1.33	9
All other forms	..	..	1		2	5	1		3	..	..	1	..	..	..	..	..	2	..	..	..		..	..	..	0 15	15

*Series 3034 did not produce true *sativums* in the F_2.
†2.00 or over.

Squareheadedness is not confined, however, to the *sativum* form. Other species, with the exception of the wild wheat, may show this character, particularly the segregates of the *durum*, the *turgidum*, and the *polonicum* types and even the *dicoccum* type. But squareheadedness in these forms is of low degree and is comparatively rare (Plate LXVII, lower).

The analysis of the F_2 forms in specific crosses presents a difficult task because a large number of specific forms appear, of which some are developed and others are very mediocre or sterile with different tendencies toward squareheadedness.

SUMMARY

Squareheadedness, being the result of a combination of growth characters, shows a complex mode of inheritance. Simple mendelian segregations were not obtained in these experiments.

In the F_3 generation there were obtained plants of different degrees of squareheadedness, ranging from forms which were distinctly compacted at the tip to forms which were denser near the base of the ear.

As a rule the range of variation in F_2 depended on the differences between the extremes of the parental ranges. The means of the F_2 approached the parental means.

The F_1 generation usually had a higher coefficient than the parental mean. Some F_1 progeny of two non-squarehead parents were even distinctly squareheads, but in F_2 none of these forms were obtained. These variations from normal expectations are ascribed to heterosis and to greater feeding area.

A coefficient of correlation of 0.465 ± 0.033 was found between width of culms and squareheadedness.

The purely spelt forms were found not to be affected by the factors producing squareheadedness. The more the spelts approached the *sativum* type, the more they were found to be affected. Speltoid forms did carry these factors, as is shown by the fact that among their *sativum* progeny a large number of squareheads of varying intensities were found.

Certain spelts when crossed with a *vulgare* form will produce a large number of squareheads in F_2. Others will produce only non-squareheaded *sativum* forms.

Squarehead forms may be produced by crossing *Triticum vulgare* with other wheat species.

THE GENETICS OF DENSITY

The discussion in the following pages deals with the genetics of compactness of the dense forms of wheat, and especially of *Triticum compactum*, the club wheat. The name *club wheat* seems to have been originally given to the squareheads, but at present it is applied almost exclusively to the *compactum* form.

The index of compactness used in this paper is the average rachis internode length. The index is found by dividing the length of the rachis in millimeters by the number of rachis internodes. The denser or more compact the head, the shorter is the length of the rachis internode.

Although there are numerous grades of compactness, the rachis internode length of what is usually called a club wheat does not exceed 2.25 millimeters. The mean density of the club used in the studies presented in this paper was about 1.4 millimeters.

INHERITANCE OF DENSITY IN CROSSES BETWEEN TRITICUM COMPACTUM AND OTHER FORMS OF THE SATIVUM GROUP

The studies of density herein discussed were made on crosses between Dale Gloria (Plate LXVII, upper, 5) and a number of lax forms consisting of both squarehead and *vulgare* types. The mean density of the Dale Gloria parent was 1.41 millimeters; the means of the lax parents were in the neighborhood of 4.50 millimeters.

The F_1 hybrids were all dense, but not quite as dense as Dale Gloria (table 16). They varied from 1.80 to 2.40, depending on the cross.

TABLE 16. SEGREGATION OF DENSITY IN CROSSES BETWEEN DALE GLORIA (COMPACTUM) AND LAX FORMS

13174a Extra Early Windsor x Dale Gloria
13173a New Soules x Dale Gloria
13172a Mealy x Dale Gloria
13214a Turkey x Dale Gloria
13215a Seneca Chief x Dale Gloria
1337a Turkish Amber x Dale Gloria
13213a Red Wave x Dale Gloria

	Degree of squareheadedness																									Mean	Number of plants
	1.3	1.5	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	5.1	5.3	5.5					
Parent plants																											
Dale Gloria	6	9	3																							1.41*	18
Extra Early Windsor														3	9	5	4	3								4.25	24
New Soules										1		4	8	5	7	4	1									3.89	30
Mealy															1	3	3	7								4.53	14
Turkey														2	3	4	3	2	1							4.34	15
Seneca Chief															1	3	3	4								4.48	11
Turkish Amber												1			3	2	4	3	8	7	3	3				4.82	34
Red Wave																	2	3	2	5	1	1				4.94	14
F_1 plants																											
13174a			2	2																						1.80	4
13173a				4																						1.90	4
13172a	Not recorded																										
13214a					2																					2.10	2
13215a				1																						1.90	1
1337a						1																				2.30	1
13213a						1	1																			2.40	2
F_2 plants																											
13174a	1	6	10	7	11	5					1	5	3	2	5	2	1	1	1							2.59	61
13173a	4	7	13	8	6		1				1	3	1	2	1	1										2.33	48
13172a		5	7	7	16	7	9	3	1		2	1	4	4	2	2	2	4								2.64	76
13214a		1	9	5	7	7	12	6	4	3					3	2	4	1	2		1					2.74	67
13215a	1	7	5	8	26	5	1	1				1	5		1	2	2	1		1						2.40	67
1337a		1	1	9	7	8	6	2	6	3			1	3	4	4	5	2	1				2			3.04	65
13213a		2	2	5	8	11	8	4	4	3					2	3	2	2	2	1			2			2.87	61

*This figure represents the arithmetical average, not the mean of the frequency distribution.

The density curves of the F_2-generation plants, unlike those of the squarehead x non-squarehead crosses, were all discontinuous, consisting of two well-defined curves. In each case the curve of the dense classes contained about three times as many individuals as that of the lax classes. The proportions of these forms are given in table 17. In five cases the

TABLE 17. PROPORTIONS OF DENSE AND LAX SEGREGATES OF THE F_2 GENERATIONS OF CROSSES BETWEEN DALE GLORIA (COMPACTUM) AND OTHER LAX FORMS

Series	Dense forms		Lax forms		Deviation	Probable error	Dev. / P. E.	Mean of dense plants	Mean of lax plants	Mean of all plants	Total number of individuals
	Number obtained	Number expected	Number obtained	Number expected							
13174a	40	45.7	21	15.2	−+5.8	±2.28	2.54	1.88	3.95	2.59	61
13173a	39	36.0	9	12.0	+−3.0	±2.02	1.48	1.74	3.74	2.33	48
13172a	55	57.0	21	19.0	−+2.0	±2.55	0.78	2.11	4.04	2.64	76
13214a	54	50.2	13	16.7	+−3.7	±2.39	1.55	2.30	4.51	2.74	67
13215a	54	50.2	13	16.7	+−3.7	±2.39	1.55	1.98	4.12	2.40	67
1337a	43	48.7	22	16.2	−+5.8	±2.36	2.46	2.34	4.40	3.04	65
13213a	47	45.7	14	15.2	+−1.2	±2.28	0.53	2.33	4.67	2.87	61
Total	332	333.7	113	111.2	−+1.8	±6.16	0.29	2 09	4.20	2 66	445

deviations from the calculated ratios exceeded somewhat their probable errors, and in two cases the deviations were well within the probable errors. Summing up the results of these seven crosses, of 445 plants obtained in the F_2 generation 332 were dense and 113 were lax; the deviation from the calculated proportions on the 3:1 basis was — + 1.8, which is about one-third of its probable error. These results show that so far as these crosses are concerned the F_2 plants segregate into dense and lax forms in 3:1 ratio, the density being dominant.

Four of these crosses, of which two were with squareheads and the other two with *vulgare*, were carried through the F_3 generation in order to test whether the assumption of the presence of one factor was correct. The results obtained are condensed and given in table 18. Of the 125 F_2 plants tested, 30 were homozygous dense, 67 produced both dense and lax forms, and 28 were homozygous lax. These figures, compared with the calculated proportions—31.2 ± 3.3, 62.5 ± 3.9, and 31.2 ± 3.3, respectively—show a very close agreement with the 1:2:1 ratio. The proportion of plants obtained in each cross taken separately agrees also with the theoretical expectancy, the largest departure being but 25 per cent more than its probable error.

TABLE 18. PROPORTIONS OF HOMOZYGOUS DENSE, HETEROZYGOUS DENSE, AND HOMOZYGOUS LAX PLANTS OF THE F_2 GENERATION OF SERIES TESTED IN THE F_3 GENERATION

	Homozygous dense forms					Heterozygous dense forms					Homozygous lax forms					Total number of plants tested
	Number obtained	Number expected	Deviation	Probable error	Dev / P. E.	Number obtained	Number expected	Deviation	Probable error	Dev / P. E.	Number obtained	Number expected	Deviation	Probable error	Dev / P. E.	
13172a—Mealy x Dale Gloria	9	9.2	−0.2	±1.8	0.11	21	18.5	+2.5	±2.0	1.25	7	9.2	−2.2	±1.8	1.22	37
13173a—New Soules x Dale Gloria	6	7.5	−1.5	±1.5	1.00	16	15.0	+1.0	±1.8	0.55	8	7.5	+0.5	±1.5	0.33	30
13174a—Extra Early Windsor x Dale Gloria	6	6.5	−0.5	±1.5	0.33	13	13.0	0	±1.7	...	7	6.5	+0.5	±1.5	0.33	26
13214a—Turkey x Dale Gloria	9	8.0	+1.0	±1.6	0.63	17	16.0	+1.0	±1.9	0.53	6	8.0	−2.0	±1.6	1.25	32
Total	30	31.2	+1.2	±3.3	0.36	67	62.5	+4.5	±3.9	1.15	28	31.2	−3.2	±3.3	0.97	125

The behavior of each individual F_2 plant of the four crosses under consideration is shown respectively in tables 19, 20, 21, and 22. Of the

TABLE 19. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13172a, MEALY (VULGARE) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev / P. E.
				Number obtained	Number calculated	Number obtained	Number calculated				
30-11	1.50	1.35	....	29	....	..	....	29			
30-21	1.53	1.66	....	22	....	..	....	22	....	....	
29-9	1.57	1.18	....	6	....	..	....	6	....	....	
29-8	1.65	1.46	....	20	....	..	....	20	....	....	
30-2	1.71	1.37	....	22	....	..	....	22	....	....	
30-14	1.73	1.52	....	24	....	..	....	24	....		
30-5	1.76	1.54	....	24	....	..	....	24	....		
30-18	1.81	1.43	....	28	....	..	....	28			
29-4	1.89	1.71	....	18	....	..	....	18	....		
30-7	1.84	1.47	3.08	24	22.5	6	7.5	30	+− 1.5	±1.63	0.92
30-6	1.85	1.72	3.41	33	32.2	10	10.7	43	+− 0.7	±1.92	0.36
30-9	1.90	1.52	3.01	34	33.7	11	11.2	45	+− 0.2	±1.96	1.00
30-8	1.95	1.69	3.56	31	30.7	10	10.2	41	+− 0.2	±1.87	0.11
29-6	2.00	1.44	3.06	18	18.7	7	6.2	25	−+ 0.8	±1.46	0.55
30-19	2.00	1.65	3.00	23	21.0	5	7.0	28	+− 2.0	±1.55	1.29
29-10	2.06	1.80	3.70	25	24.7	8	8.2	33	+− 0.2	±1.68	0.12
30-3	2.10	1.67	3.53	28	27.0	8	9.0	36	+− 1.0	±1.78	0.56
29-3	2.11	2.08	3.30	19	15.7	2	5.2	21	+− 3.2	±1.34	2.39
30-13	2.14	1.70	3.33	34	36.0	14	12.0	48	−+ 2.0	±2.02	0.99
29-12	2.19	2.04	4.03	22	18.7	3	6.2	25	+− 3.2	±1.46	2.19
30-20	2.25	1.83	3.64	22	24.7	11	8.2	33	−+ 2.8	±1.68	1.67
29-1	2.39	1.90	3.15	18	16.5	4	5.5	22	+− 1.5	±1.37	1.09
29-11	2.42	1.72	3.69	30	29.2	9	9.7	39	+− 0.7	±1.82	0.38
30-10	2.43	1.93	3.52	32	27.7	5	9.2	37	+− 4.2	±1.78	2.36
30-1	2.50	2.22	4.23	37	35.2	10	11.7	47	+− 1.7	±2.00	0.85
30-15	2.52	1.85	3.47	28	25.5	6	8.5	34	+− 2.5	±1.70	1.47
29-2	2.53	2.00	3.64	19	19.5	7	6.5	26	−+ 0.5	±1.49	0.33
30-4	2.58	1.81	3.56	27	28.5	11	9.5	38	−+ 1.5	±1.80	0.83
29-14	2.84	1.78	4.26	13	13.5	5	4.5	18	−+ 0.5	±1.24	0.40
Total heterozygous plants				517	501.7	152	167.2	669	+−15.2	±7.55	2.01
30-16	3.28	....	3.39	..	....	16	....	16	....	....	
30-12	3.55	....	3.36	..	....	23	....	23	....	....	
30-22	3.75	....	3.12	..	....	20	....	20			
30-17	3.84	....	3.43	..	....	17	....	17			
29-13	4.16	....	3.88	..	....	20	....	20			
29-5	4.27	....	3.65	..	....	17	....	17	....	....	
29-7	4.44	....	4.08	..	....	5	....	5	....	....	
Total F_3 plants....								980			

669 heterozygous plants obtained in series 13172a (table 19), 517 were dense and 152 were lax, the deviation from the calculated ratio being about twice its probable error. In series 13173a (table 20), the ratio between the probable error and the deviation from expectation is 1 : 5.22, which is rather high. In series 13174a (table 21) this ratio is 1 : 5.02, and in series 13214a (table 22) it is only 1 : 0.46. All these results, in spite of the differences between observed and calculated ratios which

TABLE 20. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13174a, NEW SOULES (CAPITATUM) x DALE GLORIA

F_2 pedigree	F_2 density	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P. E.
		Number obtained	Number calculated	Number obtained	Number calculated				
32-7	1.31	37	....	..	....	37	....	....	
31-11	1.52	23	....	..	....	23	....	....	
32-6	1.52	60	....	..	....	60	....	....	
31-3	1.55	40	....	..	....	40	....	....	
31-9	1.55	35	....	..	....	35	....	....	
32-8	1.62	41	....	..	....	41	....	....	....
31-8	1.64	24	27.8	13	9.2	37	−+ 3.8	±1.78	2.13
32-13	1.65	52	58.5	26	19.5	78	−+ 6.5	±2.58	2.52
32-14	1.68	51	54.0	21	18.0	72	−+ 3.0	±2.48	1.21
31-7	1.71	29	31.5	13	10.5	42	−+ 2.5	±1.89	1.32
32-15	1.71	93	99.8	40	33.2	133	−+ 6.8	±3.37	2.02
32-9	1.78	67	67.5	23	22.5	90	−+ 0.5	±2.77	0.18
32-16	1.81	59	63.0	25	21.0	84	−+ 4.0	±2.68	1.49
31-12	1.88	35	32.3	8	10.7	43	+− 2.7	±1.92	1.41
32-5	1.91	46	46.5	16	15.5	62	−+ 0.5	±2.30	0.22
32-10	1.95	62	63.0	22	21.0	84	−+ 1.0	±2.68	0.37
31-1	1.95	30	43.5	28	14.5	58	−+13.5	±2.22	6.08
32-2	2.00	42	39.0	10	13.0	52	+− 3.0	±2.11	1.42
31-2	2.06	40	39.8	13	13.2	53	+− 0.2	±2.13	0.09
31-4	2.09	30	33.0	14	11.0	44	−+ 3.0	±1.94	1.55
32-12	2.15	83	87.8	34	29.2	117	−+ 4.8	±3.16	1.52
32-17	....	62	69.8	31	23.2	93	−+ 7.8	±2.82	2.76
Total heterozygous plants		805	856.5	337	285.5	1,142	−+51.5	±9.87	5.22
31-10	3.40	..	....	37	....	37			
31-6	3.43	..	....	21	....	21			
32-4	3.45	..	....	56	....	56			
32-3	3.80	..	....	69	....	69			
32-1	3.87	..	....	31	....	31			
31-5	3.95	..	....	33	....	33			
31-13	4.19	..	....	24	....	24			
32-11	4.28	..	....	71	....	71			
Total F_3 plants						1,720			

they exhibit occasionally, show that so far as these crosses are concerned only one factor is involved in the production of density.

Referring to tables 19, 20, 21, and 22, it will be noticed that while in series 13172a and 13214a the proportion of dense and lax forms agreed rather closely, in series 13173a and 13174a an excess of lax forms was recorded in practically every case. In series 13173a, out of 16 heterozygous plants tested all but three yielded an excess of lax forms, while in series 13174a all but one plant yielded an excess of lax forms.

When wheat plants are grown closely together, the roots occasionally tend to intertwine, and unless the heads show variations of segregating gross characters it is not usually possible to determine whether there are two plants or only one. In crosses between dense and lax plants, in which the segregation is 3:1, out of 16 possibilities there are 9 chances

TABLE 21. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13174a
EXTRA EARLY WINDSOR (CAPITATUM) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P. E.
				Number obtained	Number calculated	Number obtained	Number calculated				
34-3	1.31	1.29	....	29	....	..	....	29			
34-8	1.40	1.28	....	25	....	..	....	25	....		
34-11	1.55	1.36	....	22	....	..	....	22	....		
33-5	1.55	1.28	....	46	....	..	....	46	..		
33-15	1.85	1.30	....	46	....	..	....	46	...		
33-9	2.00	1.28	....	39	....	..	....	39	.		
33-4	1.70	1.37	3.09	59	64.5	27	21.5	86	−+ 5.5	±2.70	2.04
33-2	1.74	1.57	3.77	56	63.7	29	21.2	85	−+ 7.8	±2.69	2.90
34-4	1.86	1.57	3.69	31	32.2	12	10.7	43	−+ 1.3	±1.92	0.68
34-6	1.95	1.54	3.31	23	24.0	9	8.0	32	−+ 1.0	±1.65	0 61
34-12	1.95	1.69	3.33	23	24 0	9	8 0	32	−+ 1.0	±1.65	0.61
34-5	2.00	1.39	3.32	18	17.2	5	5.7	23	+− 0.7	±1.40	0.50
33-6	2.00	1.54	3.59	49	51.7	20	17.2	69	−+ 2.8	±2.43	1.15
33-7	2.00	1.60	3.34	45	48.0	19	16.0	64	−+ 3.0	±2.32	1.29
33-3	2.00	1.60	3.42	45	50.2	22	16.7	67	−+ 5.3	±2.39	2 22
33-13	2 05	1.60	3.80	47	48 7	18	16.2	65	−+ 1.8	±2.36	0 76
34-10	2.11	1.69	3.48	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
33-17	2.20	1.57	3.53	48	52.5	22	17.5	70	−+ 4.5	±2.44	1.84
33-11	2.21	1.65	3.50	51	57 0	25	19 0	76	−+ 6.0	±2 55	2.35
Total heterozygous plants.....				518	558 0	226	186.0	744	−+40.0	±7 96	5.02
33-10	3.30	....	3.20	..	....	22	....	22			
34-1	3.50	....	3.35	..	....	34	....	34			
33-1	3.71	....	3 35	..	....	35	....	35			
34-9	3.95	....	3.86	..	....	18	....	18			
34-7	3.96	....	3.62	..	....	24	....	24			
33-16	4 05	....	3.33	..	....	42	....	42			
33-12	4.42	....	3.77	..	....	51	....	51	...		
Total F_3 plants								1,177			

that a dense plant will grow next to a dense plant, 6 chances that it will grow next to a lax plant (or that a lax plant will grow next to a dense plant), and 1 chance that a lax plant will grow next to a lax plant. In other words, where entangling exists due to close planting, there will be six cases in which this condition will be detected and lax and dense plants separated, and nine cases in which it will be overlooked because the heads will all be dense and will show no visible difference. If this factor of entanglement is present whereby some dense plants are overlooked, theoretically there will be fewer dense plants than are expected.

If the degree of experimental error introduced by this factor is calculated, it will be found that if, among 50 plants forming a segregating population, there are two or three cases in which a dense plant has been interlaced with its neighbor and is not separated, the differences between recorded and theoretical ratios will be about as great as those shown in tables 20 and 21.

TABLE 22. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13214a, TURKEY (VULGARE) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P. E.
				Number obtained	Number calculated	Number obtained	Number calculated				
38-8	1.72	1.46	....	68	....	..	....	68	....	....	
39-9	1.91	1.76	....	45	....	..	....	45	....	....	
38-12	1.95	1.41	....	97	....	..	....	97	....	....	....
38-14	1.95	1.49	....	85	....	..	....	85	....	....	
39-4	2.06	1.66	....	33	....	..	....	33	....	....	
38-11	2.16	1.51	....	59	....	..	....	59	....	....	
38-9	2.33	1.61	....	83	....	..	....	83	....	....	
38-13	2.39	1.58	....	57	....	..	....	57	....	....	
38-4	2.75	1.49	....	44	....	..	....	44	....	....	....
40-3	1.57	1.37	3.18	73	57.8	4	19.2	77	+−15.2	±2.56	5.94
40-6	2.11	1.65	3.23	47	41.3	8	13.7	55	+− 5.7	±2.17	2.63
38-15	2.11	1.58	3.20	35	40.5	19	13.5	54	−+ 5.5	±2.15	2.56
40-1	2.28	1.64	3.15	42	48.0	22	16.0	64	−+ 6.0	±2.34	2.56
39-3	2.35	1.67	3.28	29	31.5	13	10.5	42	−+ 2.5	±1.89	1.32
40-2	2.35	1.91	3.51	53	54.8	20	18.2	73	−+ 1.8	±2.50	0.72
39-2	2.53	1.76	3.44	52	51.7	17	17.2	69	−+ 0.2	±2.39	0.08
38-2	2.53	2.08	4.30	10	12.8	7	4.2	17	−+ 2.8	±1.20	2.33
40-7	2.57	1.92	3.77	46	42.0	10	14.0	56	+− 4.0	±2.19	1.83
38-10	2.61	1.96	3.51	30	30.0	10	10.0	40	0.0	±1.85	....
39-5	2.75	1.87	3.32	24	23.3	7	7.7	31	+− 0.7	±1.63	0.43
40-8	2.79	2.13	3.78	48	58.5	30	19.5	78	−+10.5	±2.58	4.07
38-5	2.89	2.16	4.09	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
38-7	2.90	2.23	3.72	47	45.0	13	15.0	60	+− 2.0	±2.26	0.88
40-4	2.94	2.18	3.59	48	45.8	13	15.2	61	+− 2.2	±2.28	0.96
40-10	3.00	2.20	3.83	51	48.8	14	16.2	65	+− 2.2	±2.36	0.93
39-6	3.06	2.28	3.89	73	71.3	22	23.7	95	+− 1.7	±2.85	0.60
Total heterozygous plants... ..				731	726.7	238	242.2	969	+− 4.2	±9.09	0.46
38-3	4.06	....	3.94	..	....	37	....	37			
38-1	4.11	....	4.57	..	....	12	....	12			
38-6	4.14	....	3.75	..	....	41	....	41			
39-1	4.21	....	3.41	..	....	32	....	32			
38-16	4.59	....	3.78	..	....	58	....	58			
40-5	5.29	....	3.64	..	....	91	....	91	....		
Total F_3 plants ...								1,811			

In crosses 13173a and 13174a, density was the only visible differentiating character; hence the separation of the entangling plants depended merely on that character. In series 13172a and 13214a, in which the experimental errors were practically as much on one side as on the other, the error due to entangling was reduced, respectively, by the introduction of the pubescent glume character through the Mealy parent, and by the color of chaff and the beardedness introduced by the Turkey parent. The introduction and consequent segregation of these characters enabled the author to detect the presence of more than one plant, and through their separation the degree of experimental error in these two sets of crosses was greatly lowered.

INFLUENCE OF THE DENSITY OF THE LAX PARENT IN A LAX X COMPACTUM CROSS ON THE DENSITY OF SUCCEEDING GENERATIONS

In connection with table 16 (page 836) the reader perhaps noticed that there was a tendency on the part of some F_1 and F_2 generation frequencies to be shifted somewhat toward the laxer classes while others tended to shift toward the denser classes. Since the dense parent (Dale Gloria) was the same in all seven cases, these variations, if hereditary to any extent, should be ascribed to the influence of lax parents which represent the variable factors.

The mean densities of parent and offspring are represented graphically in figure 80. The curves are arranged in the ascending order of the

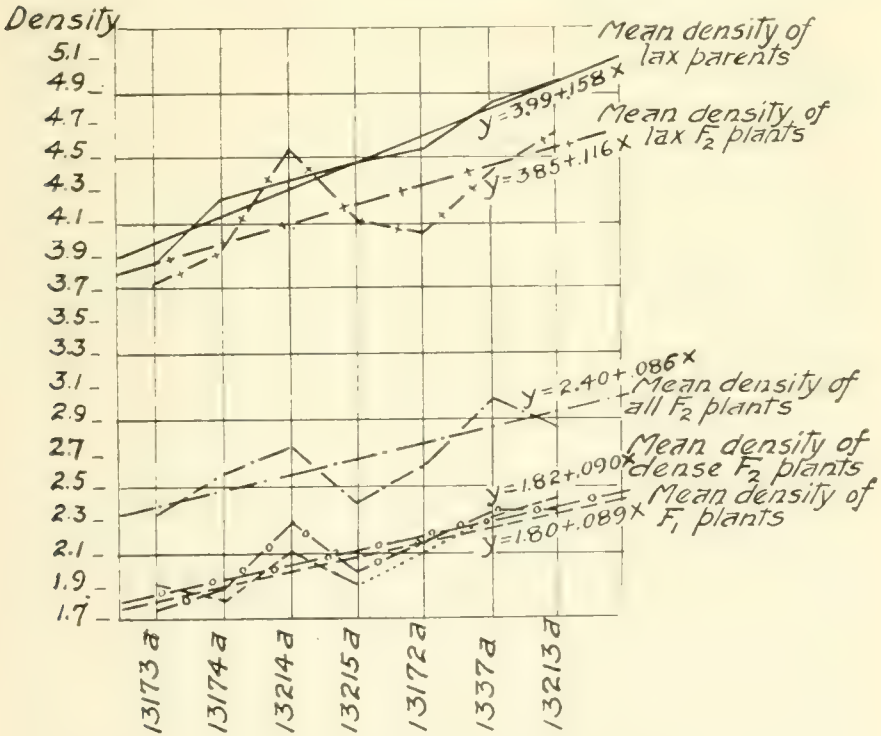

FIG. 80. INFLUENCE OF DENSITY OF LAX PARENT ON DENSITY OF F_1- AND F_2-GENERATION PLANTS

densities of the lax parents. The straight lines fitted to the curves show a general rise; that is, with the increase of the average internode length of the lax parent, the average internode length of the F_1 and the F_2 increase more or less in the same proportion.

The slopes of the fitted lines for the F_1, the total F_2, and the dense F_2 segregate, are practically the same, being 0.089, 0.086, and 0.090, respectively. Those for the lax parents and the lax F_2 segregates show also a general rise but of a higher degree. It should be borne in mind that the higher the class values, the greater is the tendency of the curve toward a higher inclination.

The curves representing the densities of the F_1 and the dense F_2 segregates follow each other very closely. The other curves also follow the same general course. Evidently the material representing the cross with Mealy was somewhat denser, because both the F_1 and the F_2 curve show a similar rise at that point. The rise of the Mealy parent is not in the same proportion.

Aside from these differences, it should be noted that the values of P_1 and F_1 are higher because they represent crops grown in different years and also because they were spaced more widely than the F_2 plants. Besides, the F_1 perhaps shows vigor due to heterozygosis, which, together with increased food supply due to the wide distances between plants, tends to increase the size of the spike without increasing the number of spikelets, which in turn tends to increase the average internode length.

RELATION OF DENSITY OF F_2 PLANTS TO THAT OF THEIR PROGENY

The comparison of the density of F_2 and of F_3 plants leads to the decision as to whether the variations in density, especially of the F_2 heterozygous plants, are hereditary or represent mere fluctuations due to external conditions. To be sure, environmental conditions, as is pointed out in the first part of this paper, have a great influence on the degree of density. The plants used in this experiment were grown on a small area, and consequently the environmental factors had practically as much opportunity to affect the density of one plant as that of another.

In comparing the density of the F_2 plants with that of their progeny, series 13214a may be taken as an example. Deductions based on this cross will apply as well as for the other crosses. The mean densities of

the F_2 parent and the offspring, as shown in table 22, are represented graphically in figure 81. Comparison of the density curves of the F_2 plants with the mean density curves of their progeny shows that, especially in the case of the heterozygous F_2 plants, there is a correlation between the density of the F_2 and that of their F_3 segregates. Since there is such a correlation between F_2 and F_3, these apparent fluctuations are

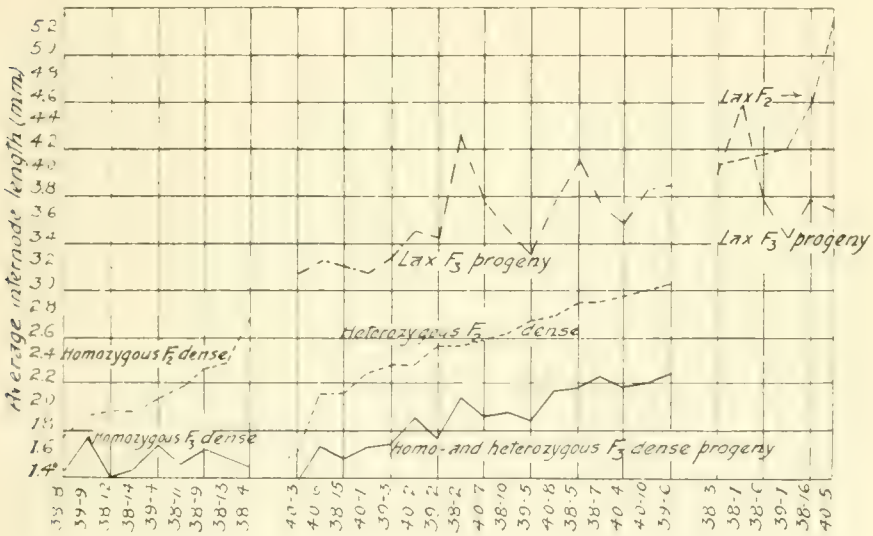

FIG. 81. COMPARISON OF DENSITY OF F_2 WITH THAT OF DENSE (HOMOZYGOUS OR HOMOZYGOUS AND HETEROZYGOUS) AND LAX PROGENY

hereditary variations. It goes without saying, then, that these F_2 heterozygous plants are not genotypically identical with respect to compactness, and that, although all the F_2 heterozygous plants have the general formula *Cc*, they carry besides this factor a group of other factors which tend to increase or decrease compactness.

RELATION OF DENSITY OF DENSE AND LAX SEGREGATES OF HETEROZYGOUS F_2 PLANTS

The presence of factors modifying the degree of density may be further demonstrated by a comparison of the curves of the dense segregates

with those of the lax segregates. This test is made on the assumption that if a group of modifiers is introduced there will be as much chance for these to be transmitted to the dense segregates as for them to be transmitted to the lax forms of the progeny of heterozygous dense F_2 plants; in other words, both dense and lax forms will receive the same dose of modifiers. Accordingly, if a set of modifiers shifts the mean of the dense segregates, say about five classes, toward a plus or a minus direction, the mean of the lax segregates should be shifted likewise, to the extent of as many classes at least, and very likely more, toward the same direction.

On examining the density frequencies shown in tables 23, 24, and 25, it will be noted that whenever the dense segregates of F_2 heterozygous plants are grouped toward the laxer classes the curve of the lax segregates corresponding to them tends also to arrange itself in that direction, and vice versa. For example, in table 23 (series 13214a), of the progeny of 40-3 the dense forms are very dense, with a mean density (table 22) of 1.37. The density of the lax form is 3.18. Comparing this with the progeny of 38-2, the mean of whose dense segregates is 2.08 and of the lax 4.30, it may be seen that whatever interfered with the compactness of the dense plants of 38-2 affected also the density of the lax forms. Throughout tables 23, 24, and 25, in which the details of the frequency distributions are given, the same phenomenon may be observed. The relation between the mean density of the dense segregates and that of the corresponding lax segregates of the F_3 progeny of each heterozygous F_2 plant of series 13214a (table 22) is shown graphically in figure 82. It is seen in these graphs that with the increase or decrease in the density of the dense plants, the density of the lax forms varies in the same direction. This is a direct evidence that besides the density factor there are also modifiers affecting the degree of density within the dense and the lax classes.

GENERAL CONSIDERATION ON THE FREQUENCY DISTRIBUTIONS OF COMPACT X LAX CROSSES

Each dense x lax cross has its own peculiar type of frequency distribution, either in the first or in later generations. The type of distribution seems to depend on the density of the parents concerned and on the

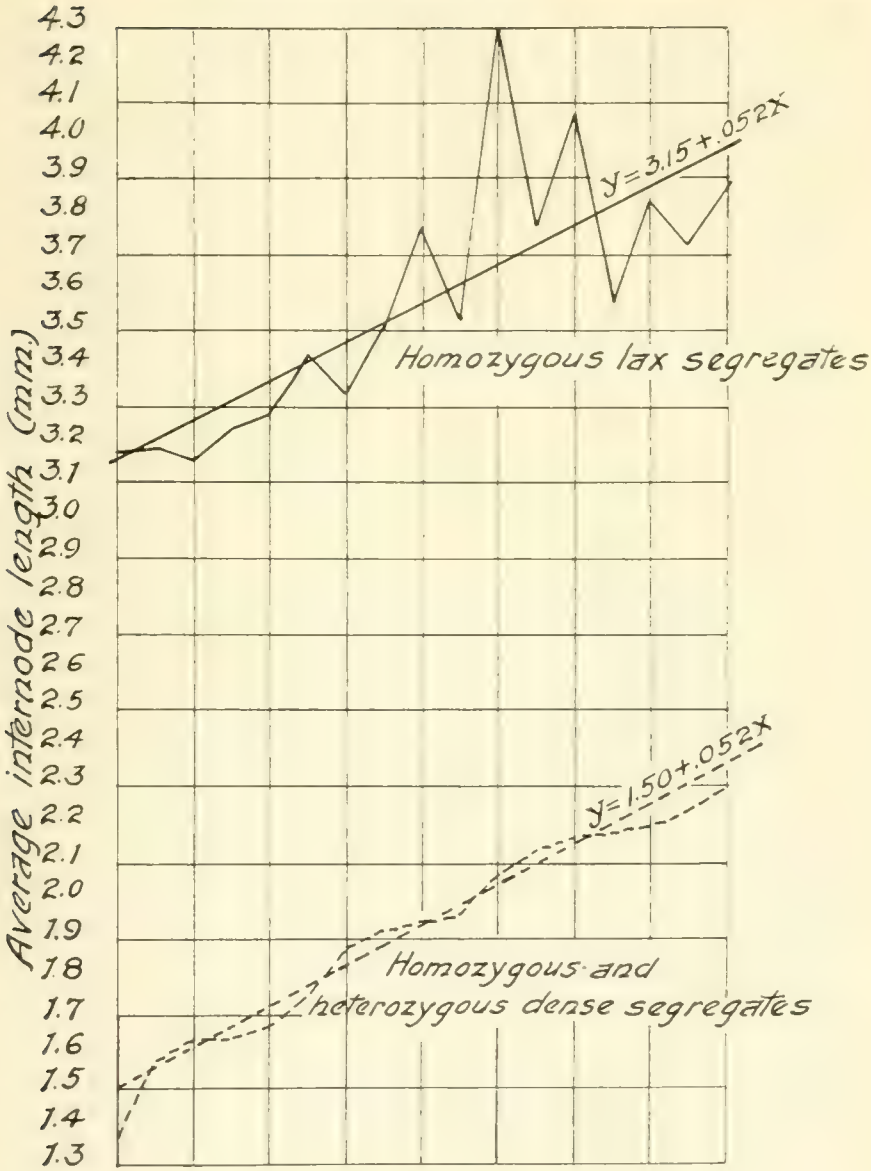

FIG. 82. RELATION OF DENSITY OF DENSE AND LAX SEGREGATES OF HETEROZYGOUS F_2 PLANTS

set of modifying factors introduced by them. In the discussion of table 16 (page 836) it was brought out that lax plants differ from one another in degree of density, and that the density of their progeny varies according to the density of the lax parent, the dense parent being the same. As to the question of modifiers, the frequency-distribution tables 23, 24, and 25 show the characteristics of the curves of each cross.

In series 13214a (table 23), although there is a gap between the dense and lax curves, in a number of cases this gap is not so evident. In figuring out the ratios the determination of the possible line of separation was a matter of judgment in some cases. Series 13172a (table 25) shows a wider gap. To a very small degree the fewness of the plants may account for it. The plants of series 13174a (table 24) show a much wider gap and the presence of two definite curves is at once seen. In crosses between dense and lax forms, all gradations between a distribution such as is shown in series 13174a, and a continuous skew curve, may be obtained.

Crosses made between semi-dense squareheads (often classified as clubs) and lax forms produce an uninterrupted curve which makes it practically impossible to separate them into dense and semi-dense, and lax genetic, classes.

Regarding the mendelian classifications of segregating lines such as those produced by the heterozygous F_2 plants of series 13214a, it will not be out of place to make a few remarks. Some workers on this subject have taken a certain class of density as a dividing line between dense and lax forms, presumably based on the classes of least frequency of the F_2 curve. While such a method may be more or less satisfactory in a cross similar to series 13174a (table 24), it is absolutely unjustifiable in genetic studies and unsuitable for the great majority of crosses in which dense or lax forms appear. In the first place, since F_2 and F_3 plants are grown in different years they do not necessarily show the same degree of density. This is shown in table 23. There is practically no heterozygous plant of the F_3 generation which produced a curve similar to that of the F_2. Theoretically about half of the F_3 curves should have approached the F_2 curve. The reason for this failure lies in the fact that the F_2 plants were grown under more favorable environmental con-

TABLE 23. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13214a, TURKEY x DALE GLORIA

		Average internode length (in millimeters)																																								
		1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0 or over
Dale Gloria				2	4	1	5	2	1																																	
Turkey																														1	1	2	1	4		2	1	1	1	1		
F_1												1	1																													
F_2							1		9	2	3	2	5	1	6	3	9	2	4	1	3	2	1									1	2	1	1	3	1	1		2		1
F_3 families																																										
Pedigree	Density of F_2																																									
38-8	1.72		3	5	7	17	21	8	5				1		1																											
39-9	1.91					1	5	10	7	10	5	4	1	1				1																								
38-12	1.95		3	8	27	18	29	7	5																																	
38-14	1.95		1	4	11	18	26	8	9	6	2																															
39-4	2.06				2	3	3	10	8	2	4						1																									
38-11	2.16		1	3	4	12	16	12	7	2	1	1																														
38-9	2.33	1		1	4	6	16	27	10	9	6	1	2																													
38-13	2.39		1	1	3	5	16	13	6	11	1																															
38-4	2.75				7	13	11	7	4	1	1																															
40-3	1.57		1	18	16	18	12	6			1	1								1			2						1													
40-6	2.11			1	6	6	2	10	5	4	7	4	1		1		1		1				1	1	1			1	2													
38-15	2.11	1	1	1	5	5	2	3	7	4	4	1	1						1	2	1	2	1	2	5	4	3															
40-1	2.28		2	2	4		6	5	8	5	5	3	2				1			3	3	4	2	1	2	1	1	1	3													
39-3	2.35				2	1	8	5	2	5	3	1	1	1						1	1	2		1	3	1	1	2	1													
40-2	2.35		1			3	4	4	6	3	8	5	5	5	7		1	1					1	3	2	2	6	2		1	1	1		1								
39-2	2.53			1	3	4	4	10	6	2	6	9	1	3	1	1	1			1	1		1		2	2	2	5	2	1												
38-2	2.53							2	1	1			1	1	1		3												1			1	2				2					1
40-7	2.57				2	5	4	2	4	3	2	6	11	2	3	1	2	1			1			1	2				1	1	1	1		1								1
38-10	2.61					2	1	2	5	1	2	3	4	4	5		1					1		1	2		1	1	1	2	1											
39-5	2.75						2	6	2	1	3	5	1	1	2	1						2			2	1	1		1													
40-8	2.79						1	4	4	5	4	2	2	3	5	6	9	3				1	1	2	1	2	2	3	1	2	5		6	2	1				1			
38-5	2.89								3	1	4	2	2	3	2	2	1			3								1				3	2	1	1		1					
38-7	2.90							2	3	5	1	1	3	6	6	7	7	2	2	2			1		2	2	1		1	1	1		1	2		1						
40-4	2.94							1	4	5	4	5	3	5	7	8	6	1		1			1		2	1	3		2	1	1	2										
40-10	3.00				1	1		3	2	6	2	2	4	3	4	6	7	7	1	1	1				1		1	1	2	1	3	4			1							
39-6	3.06							3	4	3	8	1	6	3	9	8	7	4	7	3	3	1			1	2	1	3	2	3	2		1	3	2			1	1			
38-3	4.06														1									2		3	2	5	2	1	2	1	4	4	1	3		1	2	2		
38-1	4.11																																	3		2	1	1	2		1	2
38-6	4.14																				1	2		1	2	2	2	6	8	5	3	1	2			2	1	3				
39-1	4.21																	1			2	1		1	1		7	1	3	2	2	1		1								
38-16	4.59																			1	2	1		1	2	5	5	5	5	3	5	6	4	7	1	1	1	1				1
40-5	5.29																		1	1		2	1	12	3	7	16	4	10	10	7	5	2	5	2	1	1					1

TABLE 24. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13174a, EXTRA EARLY WINDSOR x DALE GLORIA

Average internode length in millimeters

	Density of F_2	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9
Dale Gloria				2	4	4	5	2	1												
Extra Early Windsor																					
F_1									2	1	1										
F_2					1	3	3	4	6	4	3	9	3	5							
F_3 families																					
Pedigree																					
34-3	1.31		1	12	10	3	1	1	1												
34-8	1.40		5	8	5	1	5	1													
34-11	1.55			3	9	4	5	1													
33-5	1.55	3	3	16	13	6	[illegible]			1	1										
33-17	1.85		3	9	21	10	3														
33-9	2.00		4	14	12	5	1	2	1												
33-4	1.70	4	5	12	7	7	12	5	4	2	1							1	1	4	1
33-2	1.74	1		5	8	5	5	11	7	6	5	2	1								
34-4	1.86	1		1	2	2	9	4	6	2		2	1								
34-6	1.95			3	2	3	3	4	4	2	2										
34-12	1.95			2		1	3	2	4	3	7	1									
34-5	2.00		1	5	2	2	3	3		1	1								1		
33-6	2.00		2	9	2	5	8	7	6	1	5	3	1								
33-7	2.00			4	3	6	9	4	7	4	6			1		1					
33-3	2.00			2	6	4	3	12	9	2	4	1	2								
33-13	2.05			1	7	5	6	4	14	4	4	2									
34-10	2.11				5	1	3	3	1	1	2	3	4								
33-17	2.20		1	3	5	5	6	9	8	8	2	1									
33-11	2.21				3	8	5	8	10	9	3	4		1							1
33-10	3.30																			2	1
34-1	3.50																				1
33-1	3.71																			1	
34-9	3.95																				
34-7	3.96																				
33-16	4.05																				1
33-12	4.42																				

	Density of F_2	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0 or over
Dale Gloria																						
Extra Early Windsor											3	7	2	1	4	4		2	1			
F_1																						
F_2					1	1	4	1	2	1	1	3	2	2		1			1	1		
F_3 families																						
Pedigree																						
34-3	1.31																					
34-8	1.40																					
34-11	1.55																					
33-5	1.55																					
33-17	1.85																					
33-9	2.00																					
33-4	1.70	6	3	3	3	3	1	1														
33-2	1.74					2	2	9	4	2	5	2	1			1	1					
34-4	1.86				2		3	1	1		2	2	1									
34-6	1.95	1	1	3	1			3														
34-12	1.95		1	3	1	2		2														
34-5	2.00			2	1				1													
33-6	2.00	1		2		2	3	5	2	1	2	1	1									
33-7	2.00	4	1	1	6	2		3	1				1									
33-3	2.00	2	1	4	3	2	3	2	4					1								
33-13	2.05			1			2	2	3	3	2	1	2	1	1							
34-10	2.11			2	1	2	1	2					1									
33-17	2.20		2	4	3	1	3		4	1	1	1	1			1						
33-11	2.21			1	5	2	6	5	2	2	1											
33-10	3.30	1	2	11	2	1	1				1											
34-1	3.50	3	4	5	6	4	4	2	3	1		1										
33-1	3.71	1	6	4	5	7	3	5	2	1												
34-9	3.95				1	1	1	4	4	1	2		1	1					1			1
34-7	3.96				2	4	3	3	6	4	1	1										
33-16	4.05	4	4	7	8	5	4	5	3	1												
33-12	4.42			3	2	2	6	5	9	3	5	5	6	3	2							

TABLE 25. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13172a, MEALY x DALE GLORIA

Average internode length (in millimeters)

		1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8
Dale Gloria			2	4	4	5	2	1																															
Mealy																																1		3	1	2	1	6	
F_1		Not recorded																																					
F_2					1	4	3	5	4	3	9	7	4	3	4	5		3	1					1	1	1	1	3	3	1		2	1	1	2		3	1	
F_3 families																																							
Pedigree	Density of F_2																																						
30-11	1.50	1	10	5	6	3	3		1																														
30-21	1.53				3	5	6		3	3	1	1																											
29-9	1.57	2	3	1																																			
29-8	1.65	1	1	3	4	5	4	1	1																														
30-2	1.71	1	1	9	7	1	2	1																															
30-14	1.73		1	1	5	6	9	2																															
30-5	1.76		1	1	5	7	4	4	1	1																													
30-18	1.81		3	5	10	4	3	2	1																														
29-4	1.89					3	3	6	3	2		1																											
30-7	1.84		1	5	5	8	1	3		1							1		1	1				1	1	1													
30-6	1.85			4	3	3	2	4	7		7	2	1						1		2				1	2	2		1	1									
30-9	1.90		1	7	2	5	12	3	3		1						1	1	2	2	1	3										1							
30-8	1.95			3	3	3	6	2	8	1	1	2	2							1			1		2	1	1	1		2		1							
29-6	2.00		1	3	3	3	1	3		1									1		3	1	1	1															
30-19	2.00		2	1	3	2	2	4	4	3	1	1							1		2	2																	
29-10	2.06					6	4	1		6	5	1	2											1		2	2		1		1			1					
30-3	2.10			5	2	2	4	2	3	7	1	2										1	1		1	2		1		2									
29-3	2.11					1			2	3	3	1	4	2	2	1						1				1													
30-13	2.14					12	4	6	4	4	3		1					1		1		1	2	4	1	1	1	1				1							
29-12	2.19					2	2		1	2	1	7	4		1	1	1													1	1		1						
30-20	2.25				2	2	2	1	3	4	4	3	1											2	2	2	1	1	1				1		1				
29-1	2.39			3				1	1	2	4	4	3								1	1	1	1															
29-11	2.42		1	1	1	8	4	2	2	3	4	1	3												2		1	4	1				1						
30-10	2.43					1	7	2	3	3	3	7	4			2						1				1	1	2											
30-1	2.50						1	2	2	2	4	3	7	2	7	3	1		2			1								1	1		4	2		2			
30-15	2.52			1	1	2	3	1	3	5	5	5	2							1				3						1			1						
29-2	2.53						2	3	1	2	2	2	2	5											1	3	1				2								
30-4	2.58		2		2	2	2	1	3	3	6	4	2								1				1	1	4	3	1										
29-14	2.84			1	1	1	2	3	1			2	1			1														1		2			1			1	
30-16	3.28																			2	1	1	2	1	1	3	1	2	1	1									
30-12	3.55																			2	4	3	1	2	3	2	3		1	1						1			
30-22	3.75																		2	5		4	2	4	2	1													
30-17	3.84																				1		1	7	2	1	2	1		2									
29-13	4.16																						2	1			1	2	3	2	3	1	2	1		2			
29-5	4.27																			1	1	1	1	2		3	2			3						2			1
29-7	4.44																											2					1		1	1			

ditions than were the F_3. Now if, for example, density class 3.2 based on the F_2 curve (table 23) is taken as the dividing line and is used for separating the dense and lax forms of the F_3, it will be noticed that a large number of lax forms of the F_3 will be included in the dense class.

It has been mentioned that each F_3 curve has its peculiar mode of distribution. In tables 23 and 25 it is shown that the frequencies of some dense curves extend beyond the classes where the curves of some lax forms have begun. The peculiarity of each curve necessitates the taking of each curve and the separation of the dense from the lax forms at the class or the probable class of least frequency. If the density curves of segregating forms are not prepared, more trustworthy results can be obtained by classifying the forms by eye than by taking an arbitrary dividing line. This latter method can be used in cases in which the variations are discontinuous.

In specices crosses, discontinuous curves are the exception rather than the rule, and separation of dense and lax forms into two genetic classes by an arbitrary dividing line has no meaning because such a separation cannot be made even by the examination of the curves, even disregarding the fact that some specific forms which carry the density factor may be laxer than most of the *vulgare* forms.

That density is a dominant character and is inherited in the 3:1 ratio has been shown by Spillman (1902), Strampelli (1907), Wilson (1907), Von Tchermak (1910), Nilsson-Ehle (1911), Mall (1912), Parker (1914), and others. The three last-named have called attention to the fact that forms laxer and denser than the parental types are obtained also in *compactum* x *vulgare* crosses.

The use of the word *squarehead* for semi-dense forms by some authors accounts for the disagreement of their results. Von Rümker (1908) obtained from compact x non-compact crosses, compact, squarehead, and *vulgare* forms in approximately the ratio 1:2:1. No doubt the "squareheads," which proved to be heterozygous, were heterozygous club forms. Von Rümker cites another case in which the F_2 segregated into dense and lax forms approximating 3:1, there being no squarehead forms. The heterozygous forms in this cross could not be distinguished from dense forms.

Biffen's (1905) results, which are often cited as contrary to those obtained by others, seem rather to agree with Von Rümker's. Such differences as exist are due to methods and nomenclature. Biffen crossed Squarehead's Master with Red King, the average internode lengths being, respectively, 3.2 and 4.6 millimeters. The F_1 hybrid ears averaged 4.8 millimeters in internode length, and the F_2 ranged from 3.2 to 5 millimeters. In this early work the frequencies are not given, but it appears that the distribution was of the normal, or skew, type. Using 4.6 (the mean of Red King, or the internode length of this lax parent) as the dividing line, Biffen found that 78 plants were laxer than the lax parent and 22 were intermediate between the dense and the lax parent, while there was no form denser than Squarehead's Master. From this result Biffen concluded that in this case laxness was dominant. In the first place, Squarehead's Master, with an internode length of 3.2, does not fall in the *compactum* class and the cross should not be included in that category. In the second place, the use of the density of the lax parent as the dividing line seems to be too arbitrary and unjustifiable from a genetic standpoint.

Neither does Biffen's Rivet x Polish cross fall in this category, since it does not belong to the *sativum* group. In crosses of this type specific segregations occur which greatly complicate ratios. His Devon x Hedgehog cross is of the semi-dense *compactum* x lax type. The photographs shown in the article cited, and also by Bateson (1909:23), show that the F_1 is intermediate dense and the F_2 evidently approximates the 3:1 ratio, the heterozygous forms being slightly laxer than the dense parent.

Biffen's results, then, so far as the *compactum* x lax cross is concerned, may be regarded as being in accord with similar work done by others.

Since different types of dense and lax forms have been used by various investigators, their results with respect to degree of density have been different. Segregation into two distinct curves is obtained as the degree of density of the parents approaches the extremes of the dense and lax classes. As a rule, the closer the parents approach in degree of density, the more continuous the curves will be. This statement applies for crosses made within the *sativum* group. The existence of several factors producing varying degrees of density is evident.

THE NATURE OF DENSITY FACTORS

Three questions of special interest arise, regarding the nature of the density factors producing varying degrees of density in so-called pure lines. They are: (1) Is the density of the *compactum* type caused by but one factor pair, and are the degrees of density produced by the presence of modifiers? (2) Do the forms varying in degree of density carry different density factors allelomorphic to one another, or (3) Are they caused by multiple factors?

A considerable amount of work has yet to be done to answer these questions definitely, as numerous genetic analyses are necessary. A few suggestions based on experimental results can be made, however, regarding the probable nature of these density factors.

The results of all the *compactum* x lax crosses reported thus far show the presence of but one density factor; a 15:1 ratio has not yet been obtained. But in crossing a *compactum* with a somewhat dense *vulgare*, not infrequently forms are obtained which are laxer than the *vulgare* and denser than the *compactum* parent. For the sake of simplicity in previous discussions, this occurrence was ascribed to the presence of modifiers. The writer believes that these modifiers are secondary factors representing varying degrees of density. The factorial combinations according to this hypothesis, and their corresponding phenotypes, may be illustrated in the following manner:

P_1	CC dd x cc DD *compactum* slightly dense *vulgare*					
F_1	CcDd *compactum* slightly laxer than dense parent					
F_2	1 CCDD 2 CCDd	1 CCdd 2 CcDD	2 Ccdd 4 CcDd	1 ccDD	2 ccDd	1 ccdd
	12 *compactum*			4 *vulgare*		
	3 denser than dense parent	3 approximately of same density as dense parent	6 laxer than dense parent	1 same as *vulgare* parent	2 slightly laxer than *vulgare* parent	1 much laxer than *vulgare* parent

In the preceding outline, *C* stands for the high degree of compactness introduced by the *compactum* parent, and *D* for the slight degree of compactness exhibited by the *vulgare* parent. This hypothesis accounts for the production of stable forms *CCDD* denser than the *compactum* parent and *ccdd* laxer than the *vulgare* parent.

In instances in which lax stable forms somewhat denser than the lax parent appear, the phenomenon may be explained according to the same hypothesis. If the above extreme dense *CCDD* and lax *ccdd* forms taken as parents are crossed, stable forms denser than *ccdd* will be obtained according to the factorial combinations.

If there are different factors of density producing the *compactum* type, certain crosses between two *compactum* forms should give 1 in 16 or 1 in 64 lax forms. Let it be supposed that the *compactum* parents have the genotypic forms $C_1C_1c_2c_2$ and $c_1c_1C_2C_2$ where there are two different *C* factors. With two factor differences, one plant out of sixteen in the F_2 should have the $c_1c_1c_2c_2$ constitution, therefore being very lax. The writer knows of but one cross between two club forms, and from that cross, among 130 F_2 plants no lax forms were observed, although considerable variations were found within the dense classes. In this case both parents seemed to be homozygous for the same *C* factor; and the *C* factors contributed by both parents either were identical or belonged to the same allelomorphic series.

The author has evidence that the density factor of the *compactum* type may belong to a multiple series. The Black Bearded Spelt carries a density factor which may be isolated by crossing it with a lax *vulgare* form. About three-fourths to one-half of the F_2 *vulgare* forms are dense and semi-dense. In five such crosses the results have been similar. This shows that a *C* factor is carried by this particular spelt. If this factor is identical or forms an allelomorphic series with another *C* factor, the F_2 *sativums* segregating in a cross between this spelt and a club should be all dense. The fact that in such a cross lax *sativum* forms also are occasionally obtained, shows that in this case there were two distinct *C* factors involved.

Another *C* factor is carried by the *dicoccum* form known as Black Winter Emmer. When this form is crossed with a *vulgare* it throws

a certain proportion of distinctly dense *sativum* individuals. The F_2 plants from eight such crosses were examined and compact forms were recorded in every case. As in the preceding instance, in the F_2 derived from two Black Winter Emmer x club crosses, consisting of about 150 F_2 individuals, soft lax vulgare types could be counted, although most of the *sativum* types were dense. Here again it appears that, as in the preceding cross, two different non-allelomorphic multiple *C* factors were introduced.

Summarizing the foregoing discussion, it is apparent that:

1. There are density factors each producing shortening of the rachis internode in different degrees. These may be present in addition to the *compactum* factor.

2. There is as yet no sufficient evidence that some *compactum* factors may form an allelomorphic series. Neither is there any evidence that such series may not exist.

3. There exists in wheat more than one density factor belonging to multiple series. If such multiple density factors are present, eventually 15 : 1, 63 : 1, and other ratios will be obtained from *compactum* x *vulgare* crosses.

FACTORS PRODUCING SQUAREHEADEDNESS AS COMPRISING ONE OF THE GROUP OF FACTORS MODIFYING DEGREE OF DENSITY

A modifier, as generally held, may be a factor affecting a particular character quantitatively, the presence of which is detected from the degree of modification of the character which it modifies. In a broad sense, however, any factor or character whose presence affects or even inhibits more or less the expression of another character should be regarded as a modifier.

The irregularities among the F_2 density curves of dense x lax crosses shown in this study were ascribed to the presence of modifiers, as the genetic analyses applied to the crosses showed conclusively the presence of but one density factor. Proofs that these variations were hereditary, and not caused by environmental conditions, were also given.

The nature of one of these modifiers, the character for squareheadedness, may here be considered. In crosses in which a non-squarehead was involved, it was noticed that there was an independent segregation of

density and squareheadedness, and that whenever the latter character was present, whether the plant was dense or lax, there was, as a rule, a reduction of the average internode length.

Density notes derived from series 13172a are summarized in table 26. This cross, it will be recalled, is between Mealy, a lax non-squarehead,

TABLE 26. MEAN DENSITY OF F_3 LAX PLANTS CLASSIFIED ACCORDING TO PROPORTION OF SQUAREHEADS AND VULGARE FORMS. SERIES 13172a

All squareheads		More squareheads than *vulgare*		Squareheads = *vulgare*		More *vulgare* than squareheads		All *vulgare*	
Pedigree	Density	Pedigree	Density	Pedigree	Density	Pedigree	Density	Pedigree	Density
30-19	3.00	29-1	3.15	29-3	3.30	29-5	3.65	29-2	3.64
30-22	3.12	29-6	3.06	....	....	29-14	4.26	29-7	4.08
..	....	29-13	3.88	....	....	30-1	4.23	29-10	3.70
		30-6	3.41	....	....	30-8	3.56	29-11	3.69
		30-7	3.08	....	....	30-10	3.52	29-12	4.03
		30-9	3.01	....	....	30-16	3.39	30-3	3.53
		30-12	3.36	....	....	30-17	3.43	30-4	3.56
		30-13	3.33	....	....	....	....	30-15	3.47
			....	....	....	....	....	30-20	3.64
Mean and average error	3.06±0.04		3.28±0.07		3.30		3.72±0.11		3.71±0.05

and Dale Gloria, a dense squarehead. In this cross both density and squareheadedness segregated independently. The table shows the density of the lax forms of the F_3-generation lines arranged in five classes, according to the observed proportions of squareheads to non-squareheads. In the first class are included the F_3 plants which consisted of squareheads only; the second class includes the pedigrees that produced more squareheads than *vulgare* forms; the other three classes represent progenies consisting of an equal number of these two forms, of an excess of *vulgare*, and of only *vulgare*, respectively.

By averaging the degree of density of each group it is found that the average internode length increases inversely with the proportion of squareheads. The average internode length of the squareheads was 3.00 ± 0.04, while that of the plants producing an excess of squareheads was 3.28 ± 0.07. The densities of the class yielding more *vulgare* than squareheads and that producing only *vulgare* were 3.72 ± 0.11 and 3.71 ± 0.05, respectively. The difference in the average internode length of the extreme classes was 0.65 ± 0.06. Comparison in terms of the average of the means of these two classes, shows this difference be-

tween the density of pure squareheads and that of pure *vulgare* to be equal to about 20 per cent of their means, which is rather remarkable.

Were the lax plants of the F_3 generation all or practically all squareheads, one would expect the elimination of variations as great as those found in the crosses between *vulgare* and dense squareheads. Series 13174a (table 24, page 850), which represents a cross between a squarehead and a dense squarehead, shows the absence of shifting of the curves back and forth, so evident in tables 23 and 25, which represent dense squarehead x *vulgare* crosses.

Although the variations introduced by the presence of both *vulgare* and squarehead forms is eliminated in cross 13174a (table 24), other modifiers must be present because the curves still show inheritable variations. The nature of these remaining modifiers is not as yet known.

It is not difficult to explain how squareheadedness increases density. Physiological studies show that squareheadedness, which is brought about by the shortening of the terminal internodes, is due to contact and pressure caused by the differential rate of growth of parts of the plant surrounding the spike during its earlier periods of growth. If, during the process, the terminal internodes fail to attain their normal size, that part of the head will be denser than it would have been if the plants were allowed to grow normally. This shortening of internodes of the terminal part of the head is the direct cause of the decrease of the average internode length of the entire head.

RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2-GENERATION PLANTS

The modes of inheritance of squareheadedness and of density have been discussed separately herein. It is necessary now to illustrate the relation between these two characters in crosses in which both of these characters have been introduced. Series 13172a, 13214a, 1337a, and 13173a (tables 27, 28, 29, and 30, respectively), which have already been considered, will be used again as examples, because each illustrates a different mode of inheritance.

Before examining the behavior of the F_2 plants, the distribution of the parent plants with respect to density and squareheadedness may be reconsidered. This distribution, although based on few numbers, is shown graphically in figure 83. The plants recorded do not represent samples of

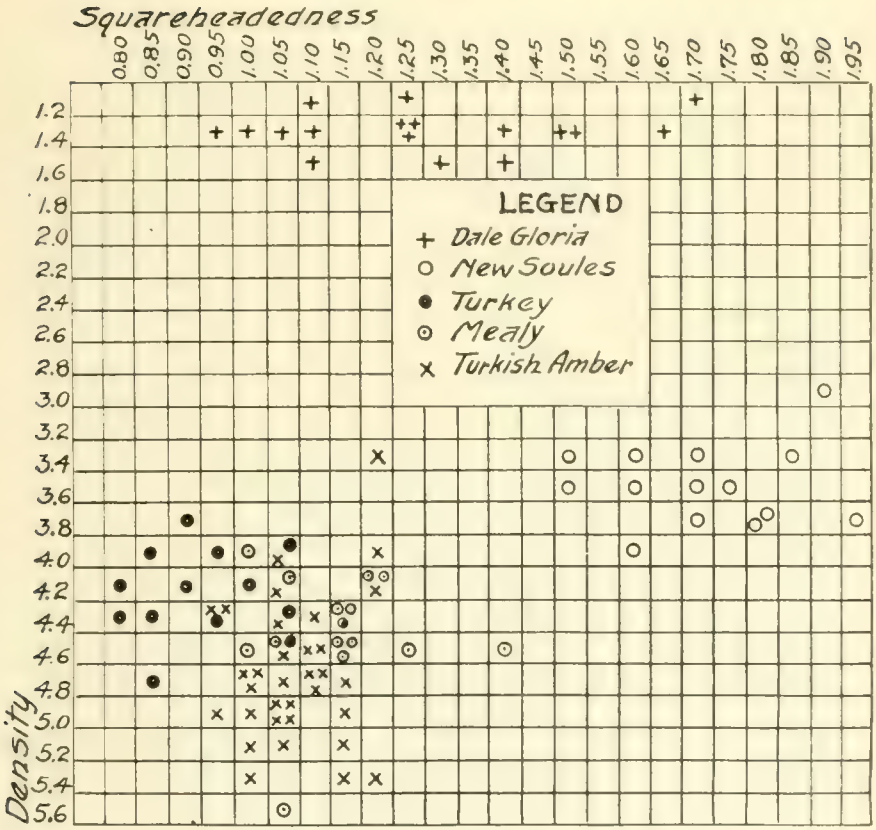

FIG. 83. DISTRIBUTION OF PARENTAL PLANTS WITH RESPECT TO DENSITY AND SQUAREHEADEDNESS

the varieties used in making the crosses; they are the progeny of each of the plants used as parents.

Dale Gloria, it is seen, is distributed within a very narrow range with respect to density, but within a wide range with respect to squareheadedness. This latter range does not represent the genotypic range of the variety, if one may be allowed to use that expression. The length of the rachis itself is about 2 to 3 centimeters. If the terminal spikelets are ster-

ile, as often happens in dense clubs and less frequently in lax forms, this sterility and rudimentary condition will keep the terminal rachis internodes from developing further while the other internodes continue their growth. A head of this type will have a high coefficient of squareheadedness. If, on the contrary, the terminal florets develop vigorously, the increase in the size of the grain will tend to stretch the internodes somewhat. With a vigorous growth of the grain is associated a relative growth of the adjacent internodes, and with as short a head as that of the club in question it does not take much increase in internode length to lower the squareheadedness of some individuals down to classes 1.00 to 1.25.

The distribution of New Soules is entirely different from those of the other lax plants used in the crosses. It is somewhat more toward the denser classes and falls distinctly within the squarehead classes.

Turkish Amber is a *vulgare*, but its average internode length is greater than that of any other of the forms represented.

TABLE 27. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13172a, MEALY x DALE GLORIA

(Mean dense plants, D=2.01, Sq.=1.34; mean lax plants, D=3.95, Sq.=1.23)

Density \ Squareheadedness	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75
1.5					1					1	1	1					1		
1.7								1				2	2		2	1			
1.9						1			1		1		1		2	1			
2.1					1			3	4	1		3	1	1		1			1
2.3		1			1	1			1		1			1		1			
2.5							1	1	2	2		1		1	1				
2.7							2	1											
2.9						1													
3.1																			
3.3								1						1					
3.5											1								
3.7				1						1	1								
3.9								2					1		1				
4.1					1					1									
4.3					1														1
4.5	1	1																	
4.7				1	1			1				1							

Mealy has practically the same distribution as Turkish Amber but is somewhat less lax.

Turkey is the least lax in the *vulgare* group and is located very much toward the non-squarehead classes.

The mode of inheritance which might generally be expected in *compactum* x *vulgare* crosses is that of the Mealy x Dale Gloria series (table 27), which shows a wide range of distribution with respect to squareheadedness. Theoretically, since Dale Gloria carries the factors responsible for squareheadedness and Mealy does not, both density and squareheadedness would be expected to segregate independently, which happens in this case. Using, for practical purposes, class 1.30 or 1.35 as a dividing line, it is seen that there are about as many individuals on the side of squareheadedness as on the side of non-squareheads. By using as a guide the distribution of the Mealy parent shown in figure 83, it becomes very evident that in this cross the character of squareheadedness has been introduced among the non-squareheads. The mean value of squareheadedness of the lax parent is 1.14 and that of the lax plants of the cross is 1.23, showing an increase of 0.09. While out of 15 Mealy parental plants (figure 83) there was but one individual in the squarehead classes in the F_2 generation, out of a total of 20 plants there were about four or five times more individuals in these classes. In table 26, which represents the same cross, it has been shown that some of these lax squareheads remained stable.

The distribution when Turkey was the lax parent (table 28) was strikingly different from that in the case of Mealy. In the Turkey x Dale Gloria cross, no lax squareheads appeared.

On comparing the dense classes of tables 27 and 28 with respect to their squareheadedness distribution, it is seen that the entire distribution has been shifted to the left in the latter table. The mean squareheadedness of Dale Gloria is 1.28; that of the dense plants of the cross is 1.17, showing a shifting of 0.11 toward the non-squarehead classes. While the squareheadedness of the dense form is affected by that of the lax forms, the difference in the coefficients of the lax parent and the lax segregates, these being 0.92 and 1.00, shows that the lax segregates are in turn influenced to some extent by the squareheadedness of the dense parent.

TABLE 28. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13214a, TURKEY x DALE GLORIA

(Mean dense plants, D=2.18, Sq.=1.17; mean lax plants, D=4.23, Sq.=1.00)

Density	Squareheadedness 0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50
1.5															1
1.7				1	1	1			2			1	1		
1.9				1					1		1	2			
2.1								1	1	2	2			1	
2.3						1			1	1	2				1
2.5					4	1		3	3					1	
2.7			2	1	1			1			1			1	
2.9			1			4									
3.1						2									
3.3															
3.5															
3.7															
3.9															
4.1	1					1			1						
4.3			1		1										
4.5					2		2								
4.7				1											
4.9			1		1										
5.1															
5.2					1										

In the cross in which Turkish Amber was used (table 29), the squareheadedness of the lax segregates occupies practically the same position as that of the lax parent itself, the values of squareheadedness of the lax parent and the lax segregates being 1.04 and 1.07, respectively. This slight shifting toward the non squarehead classes may well be disregarded. Unlike the condition in the preceding cases, the dense forms showed no visible effect of the lax parent. The mean squareheadedness of the dense segregates, instead of being less, was slightly greater than that of the dense parent and practically the same as in series 13172a.

In the fourth cross (table 30) the lax parent was New Soules, a distinct squarehead. The lax segregates of this cross were all squareheads, and with regard to density they occupied the same position as the lax squarehead parent (figure 83).

Incidentally it should be noted from this table that, while the range

TABLE 29. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 1337a, TURKISH AMBER x DALE GLORIA
(Mean dense plants, D=2.23, Sq.=1.35; mean lax plants, D=4.30, Sq.=1.07)

Density \ Squareheadedness	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80
1.5						1													
1.7								1											
1.9						1	1	4			1	1	1						1
2.1					1	1	1	1		1			1		1				
2.3					1			1	1	1		2	1	1					
2.5								1	1	1	1						1		
2.7										2									
2.9					1	1	1			1	1								
3.1													1	1	1				
3.3																			
3.5																			
3.7					1														
3.9			1		1						1								
4.1	1			1	1				1										
4.3		1		1	1	1													
4.5	1		1	2				1											
4.7				2															
4.9			1																
5.1																			
5.3																			
5.5			2																

of density of the dense segregates of other crosses extends as far down as class 3.1, that of this cross (table 30) is confined within classes 1.3 to 2.1 with but one individual in class 2.5. This difference is accounted for by the higher degree of density of New Soules (figure 83) as compared with those of the other lax forms.

Recapitulating the points of interest brought out in the discussion of these four tables, the following general deductions can be made:

1. The factors of density and those of squareheadedness are totally independent of each other. They segregate and recombine independently.

2. The wheat varieties of the *sativum* group have different degrees of density and of squareheadedness. Even among the *vulgare* plants this latter form of compactness, as measured by its coefficient, varies. In

TABLE 30 RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13173a, NEW SOULES x DALE GLORIA
(Mean dense plants, D=1.64, Sq.=1.43; mean lax plants, D=3.64, Sq.=1.59)

Density	Squareheadedness 1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85
1.3	1				1											
1.5	1					2		1	1						1	1
1.7	2			1	1	1	1		1		1			1	1	
1.9			1	1	1		2	1								
2.1						1	1		1		1			2		
2.3																
2.5						1										
2.7																
2.9										1						
3.1																
3.3											1	1				
3.5												1	1			
3.7							1									
3.9								1								
4.1								1								
4.3																1

crosses in which one parent is the same, not all *vulgare* nor all squareheads nor all dense forms produce a frequency distribution of squareheadedness or of density of the same type and within the same range. Whether the range will remain approximately in the same location, or will shift one way or the other, is determined to a great extent by the degree of squareheadedness or of density of the different forms of *vulgare* or squareheads, as the case may be, which are involved in the cross.

3. There are exceptions to the general rule stated above. In series 1337a there was a visible segregation of density but not of squareheadedness. In this case there was evidently interference by another factor.

Nilsson-Ehle (1911) considers the inheritance of squareheadedness and gives a factorial explanation to account for the apparent proportion in which it appeared in some of his crosses. But, while Nilsson-Ehle used the term *squarehead* for lax forms—which have a comparatively shorter average internode length than the *vulgare* forms—that term is applied in the present paper to forms showing a relative density of the

middle and the upper third of the spike of about 1.33 or over, irrespective of the average internode length. It is not possible to compare Nilsson-Ehle's results and hypothesis with those from this study.

RELATION OF LENGTH OF RACHIS TO DENSITY IN HYBRID PLANTS

Length of rachis is dependent on two factors, namely, the number of internodes and their length. If the number of internodes in a population is more or less constant, as has been the case in all the crosses between Dale Gloria and other forms considered herein, the length of the rachis is directly proportional to the average internode length. This is so obvious that it needs no illustration.

If both factors are made variable by the selection of parents which vary both in number and in length of internodes, then there is no correlation between length and density. As an illustration a cross may be cited which was made by the writer for this purpose. This cross was Silver Club x *Aegilops ovata*. Silver Club (Plate LXVII, upper, 3) is a club wheat from four to five centimeters long, with about seventeen to twenty internodes. The Aegilops (Plate LXVII, upper, 1) also was short, like the club wheat, but had only six internodes of an average length of about six to seven millimeters. The basal internodes were the shorter, their spikelets being rudimentary.

Unlike the parents, the F_1 plants all had long heads, resembling the spelt wheat. Three plants obtained in the F_2 also were lax. The point of interest in this cross was that the F_1 and F_2 plants did not inherit length of rachis from their parents, but number and length of internodes. The F_1 heads usually had from twelve to fourteen internodes from six- to seven millimeters in length. The three F_2 plants showed some variation in length. In the F_1 plants, both characters being intermediate, the heads were necessarily much longer than in either parent. It would be expected, if sufficient F_2 plants were obtainable, that the plants would segregate with respect to both characters into short heads dense and lax, that is, with many and with few internodes, and also comparatively long heads dense and lax, with possible intermediate forms.

In this connection it may be pointed out that what has been called vigor due to heterosis in wheat is often the appearance of unusually long heads in F_1 or later generations in crosses with certain emmers.

These are, as a rule, somewhat dense and bear some thirty internodes to the spike. Hence the question is rather one of number of internodes and internode length. The plants that combine the internode length of the *vulgare* parent with the number of internodes of the emmer must necessarily be unusually long.

In actual practice, in a cross such as the above a considerable number of synthetic spelts appear. These spelts have the peculiarity, as is shown later, of producing internodes longer than those of the lax parent. The appearance of this new type helps to increase the proportion of unusually long heads.

RELATION OF LENGTH OF CULM TO RACHIS LENGTH AND DENSITY

In a pure line of wheat there is practically no correlation between culm length and density, but there is a correlation between culm length and length of rachis. The plant that produces a short culm due to unfavorable environmental conditions naturally produces a small head; but such a head as a rule has fewer rachis internodes than the mean of the line, and therefore, although the undeveloped head is short, its density has not been affected to any extent because the number of rachis internodes has decreased more or less proportionately.

The writer's studies of the relation of culm length to density were made on series 1321.4a, because this line produced practically no squareheads. Squareheading, it has been shown, unless it is due to favorable growth conditions, has a tendency to shorten the average rachis internode length. There being no squareheads in the material used, that factor was eliminated.

The question of the relation of culm length to other characters of the head is of interest from both the economic and the genetic viewpoint. Because of the many phases to which this problem of density has led, it was not possible in this investigation to study the relation of culm characters as intensively and extensively as the subject deserves. Sufficient data have been obtained, however, to give an idea of the general behavior of this character.

Due to the great variability of culm length, the preliminary studies were made with a number of progenies of F_2 plants each of which had yielded on an average about 60 individuals. The frequencies of the

TABLE 31 RELATION BETWEEN CULM LENGTH, RACHIS LENGTH, AND AVERAGE INTERNODE LENGTH

Pedigree		Culm length (centimeters)	31–35	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	101–105	106–110	111–115	116–120	121–125	126–130	131–135	136–140	141–145	146–150	151–155	156–160	161–165	166–170	171–175	176–180	181–185	186–190	191–195	196–200	201–205	206–210	211–215	Number of plants	Mean
		Rachis length (centimeters)	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	24–25	25–26	26–27	27–28	28–29	29–30	30–31	31–32	32–33	33–34	34–35	35–36	36–37	37–38		
		Average internode length (millimeters)	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	150–159	160–169	170–179	180–189	190–199	200–209	210–219	220–229	230–239	240–249	250–259	260–269	270–279	280–289	290–299	300–309	310–319	320–329	330–339	340–349	350–359	360–369	—	+
38-3	Culm		..	..	..	..	1	..	..	1	..	5	1	..	8	2	3	4	2	5	2	..	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	40	87 44
	Rachis											1		1	1	5	3	5	9	5	5	2	1	1	1															40	8 14
	Av. internode									1					2	5	5	3	8	5	3	3	2																	37	4 01
38-4	Culm		2	3	3	3	3	9	10	5	4	2	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	46	69 52
	Rachis		..	..	14	19	8	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	46	3 03
	Av. internode		..	..	7	24	11	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	44	1 52
38-5	Culm		..	..	..	..	..	1	5	3	5	1	2	4	4	2	3	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	34	79 53
	Rachis		..	..	..	..	3	4	5	4	5	5	3	3	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	34	4 91
	Av. internode		..	..	..	..	3	5	4	5	3	..	3	..	..	..	1	..	5	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	32	2 75
38-6	Culm				1			2	1	4	2	1	4	1	4	4	6	1	3	1	4	1	1		1														42	83 71
	Rachis											1	1	3	4	5	4	1	6	5	3	5		3		1														42	8 01
	Av. internode		..	..	..	..	..	..	..	..	..	..	1	2	3	4	14	8	3	..	3	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	41	3 80
38-7	Culm		1	..	..	..	1	1	5	6	4	7	8	2	6	4	2	4	4	4	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	63	81 16
	Rachis		..	..	..	1	4	2	11	9	12	4	6	4	2	..	2	..	1	..	1	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	63	5 36
	Av. internode		..	..	..	..	5	6	4	12	14	4	2	1	2	3	1	2	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	60	2 61
38-8	Culm		1	2	1	5	6	9	7	6	7	2	5	7	5	5	3	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	72	75 53
	Rachis		..	5	13	27	25	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	72	3 05
	Av. internode		..	3	12	38	14	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	69	1 51
38-9	Culm		..	1	..	4	1	4	8	7	11	10	8	8	6	9	5	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	85	77 59
	Rachis		..	1	5	18	29	20	11	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	85	3 47
	Av. internode		..	1	5	22	37	15	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	83	1 66
38-10	Culm		1	..	..	..	1	..	1	1	1	2	3	1	4	4	2	1	5	5	2	3	2	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	42	87 09
	Rachis		..	..	..	4	3	6	5	7	3	5	1	..	1	..	6	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	42	4 91
	Av. internode		..	..	..	3	7	3	7	9	1	..	..	1	3	1	2	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	40	2 39
38-16	Culm		..	..	..	..	..	..	..	..	..	..	1	3	4	1	7	3	6	6	5	5	4	3	1	2	2	2	2	..	..	..	..	..	..	..	..	..	..	57	93 77
	Rachis		..	..	..	..	..	..	..	..	..	..	4	3	..	8	5	14	5	4	5	4	1	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	57	7 97
	Av. internode		..	..	..	..	..	..	..	..	..	..	3	1	6	10	8	8	10	8	2	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	58	3 83
40-4	Culm		..	..	..	..	..	..	1	2	..	1	..	1	2	3	4	4	5	7	8	6	5	7	3	3	1	1	..	..	..	..	..	..	..	..	..	..	..	64	93 59
	Rachis		..	..	..	1	3	9	12	8	10	7	..	2	1	4	3	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	64	5 06
	Av. internode					..	5	7	8	12	14	1	1	1	2	4	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	61	2 52
40-5	Culm		..	..	..	..	..	..	..	1	..	3	..	8	4	7	7	4	12	9	4	4	10	6	6	3	3	1	1	..	..	..	..	..	..	..	..	..	..	93	92 59
	Rachis		..	..	..	..	..	1	..	..	1	11	7	9	13	15	9	6	5	11	..	3	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	94	7 05
	Av. internode		..	..	..	..	..	..	..	..	..	1	1	3	15	23	14	17	7	7	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	91	3 69
40-6	Culm		..	..	..	..	..	..	..	2	2	5	3	4	7	8	4	9	3	4	3	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	56	85 32
	Rachis		..	..	7	10	9	12	7	3	..	2	2	..	1	..	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	56	3 95
	Av. internode		..	..	7	8	15	11	5	1	1	1	..	1	2	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	55	1 93
40-7	Culm		..	1	..	3	4	..	6	4	3	..	7	6	5	6	2	4	2	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	57	78 92
	Rachis		..	..	2	2	8	7	10	5	7	6	..	1	1	1	2	..	1	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	55	4 69
	Av. internode		..	..	2	7	6	5	17	5	3	1	1	..	3	..	1	2	1	..	1	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	56	2 29

three characters, culm length, rachis length, and rachis internode length, are shown in table 31, together with their means. The F_3 lines included in this table are arranged according to the order in which they were planted—38-3, 38-4, 38-5, and so on, representing successive rows of plantings. An inspection of the table shows that these three characters—length of culm, length of rachis, and average internode length—are more or less closely correlated. As a rule the lines with long culms produced lax plants and those with short culms yielded dense plants. It is seen from the curves in figure 84, prepared from the data in table 31, that

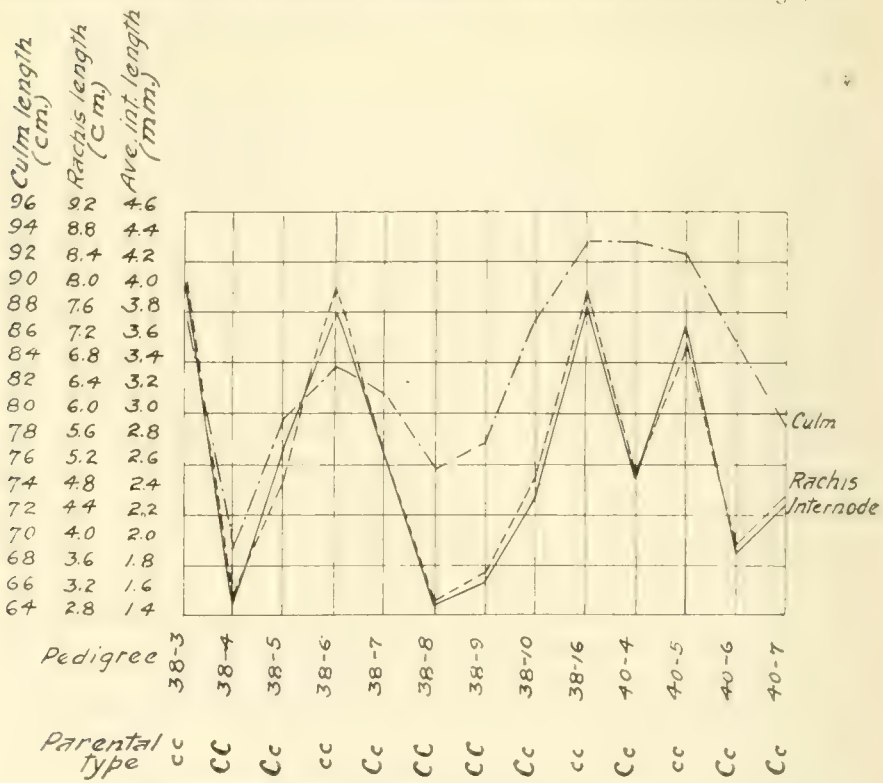

FIG. 84. AVERAGE CULM, RACHIS, AND INTERNODE LENGTH OF SOME F_3 FAMILIES OF SERIES 13214a

The curves show the relation of culm length to rachis and internode length. The order of the families corresponds to the order in which they were planted

when the mean of one of the characters decreases or increases, the others vary as a rule in the same direction.

There being no inherited variation in number of internodes (which averages about 20 to the spike) in the F_3 lines, the curves of rachis length and average internode length follow each other very closely. The curve of the culm length, although in a general way varying with density, shows certain irregularities, especially in the case of lines 38-6 and 40-4. The former is a homozygous lax type and the latter is heterozygous; yet the mean culm length of the former is considerably less than that of the latter, although theoretically it should have been greater. The possibility of the effect of environmental conditions being out of the question, it appears that there is a segregation of culm length independent of the dwarfing caused by the presence of the *C* factor. This statement is made as a suggestion only, since at the present time no definite explanation can be given.

A fact which seems rather interesting is that the *C* factor does not shorten the culm length in the same proportion as it shortens the rachis length. The averages of the rachis and culm lengths of the homozygous lax (*cc*) plants were about 7.7 centimeters and 89 centimeters, respectively. The presence of the double dose of the *C* factor (in 38-4, 38-8, and 38-9) shortened the rachis length to an average of 3.2 centimeters and the culm length to about 74 centimeters, a shortening of 58 and 17 per cent, respectively, from the general average. In other words, while the rachis length was shortened by the *C* factor by more than one-half, the culm length was shortened but one-sixth.

Studies of the characters of dense and lax segregates have led the author to believe that the *C* factor is a dwarfing factor, shortening, besides the culm length, the rachis length, and the rachis internode length, a number of other characters such as length of glumes, length of kernels, length of awns, and length of culm internodes. These two last-named characters have not been studied carefully by the author. Sapehin (1910) and his collaborators, who studied the correlation between density and culm internode length, claim that there is a significant positive correlation between these two characters. From the present studies it seems apparent that the shortening of the culm as a result of the pres-

ence of the factor for density, is due not to the reduction in number of culm internodes, but to the reduction in length of the culm internodes, the number of these internodes remaining more or less constant. In this respect the phenomenon of the shortening of the culm is similar to that of the shortening of the rachis. It has been demonstrated by various workers that in maize also dwarfing causes the shortening of the internodes of the stalk without necessarily affecting their number.

In a general statement such as is made here regarding the presence of a correlation between density of the head and shortness of the culm, it is not intended to convey the idea that dense plants or varieties are all to be short, and lax plants tall. The cardinal points brought out are (1) that when the factor of density or its absence has been introduced in a progeny through hybridization, provided there are no interfering factors, the dense plants will be more likely to have short culms than the laxer plants; and (2) that this shortening of the plant is caused, not by the reduction in number of culm internodes, but by the reduction in their length. It should be borne in mind, however, that these characters are affected by environment. From a genetic viewpoint the exhibition of a quantitative character in an individual plant is of little value especially if this is affected by environment. The comparative height of a plant is determined by the behavior of its progeny.

CORRELATION BETWEEN AVERAGE INTERNODE LENGTH AND LENGTH OF STERILE GLUMES

One of the proofs that the density factor is a dwarfing factor is found in the high degree of correlation existing between the average internode length and the length of the sterile glumes. The material for the study of this correlation consisted of the spelt plants of series 13255a-15, representing a cross between Dale Gloria and White Spelt. This F_3 line segregated into dense and lax *sativums* and spelts. In the data here only the spelts are represented. The spelts were selected primarily because the glumes could be readily removed from the spikelets, as they break off uniformly at the base of the glume at a definite region just below the heel. With *vulgare* forms the taking of measurements is somewhat more laborious. The measurements of the glumes recorded here rep-

resent the average of the length of opposing sterile glumes on the same spikelet at a distance from the base of the spike of about one-third the length of the rachis. This precaution was taken because the glumes shorten as they approach the distal or the basal part of the head.

The correlation between average internode length and glume length is represented in table 32. The correlation coefficient here is 0.838 ±

TABLE 32. CORRELATION BETWEEN DENSITY AND LENGTH OF STERILE GLUMES (Series 13255a-15, Dale Gloria x White Spelt; only the spelts measured)

Average internode length (in millimeters)	Length of glumes (in millimeters) 6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5
1.5	1	1	1						
2.0		3							
2.5		3	6						
3.0		1	1	3	2				
3.5					1				
4.0					2				
4.5				1	2	1	1	2	
5.0						1		1	1
5.5							1	1	
6.0					1	1			1

r = 0.838±0.039

0.039, which shows significantly that in this particular cross the factor decreasing rachis internode length is the one causing the shortening of glumes. The relation of density to glume length may be readily seen on heads 6, 7, and 8 in Plate LXVII (upper), which show the grades of density and consequently of glume length.

CORRELATION BETWEEN AVERAGE INTERNODE LENGTH AND LENGTH OF KERNELS

The same degree of correlation exists between density and length of kernels as between density and glume length. The measurements of the length of the kernel as here recorded represent the average length of the first and second kernels developed on the basal florets. Of these two kernels the first was very often longer than the second. In cases in which either the first or the second basal floret had not produced seed, the third seed was not measured in its stead because the third seed is always likely

to be smaller. In such cases a different spikelet was chosen, the samples being taken always at a distance from the base of the head of about one-third the length of the rachis.

Correlating these two characters as shown in table 33, a correlation

TABLE 33. CORRELATION BETWEEN DENSITY AND LENGTH OF KERNELS (Series 13255a-15, Dale Gloria x White Spelt; only the spelts measured)

Average internode length (in millimeters)	Length of kernels (in millimeters) 5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0	7.2	7.4	7.6	7.8
1.5		1			1		1					
2.0	1			1	1							
2.5	1			2	5	1						
3.0				3	1	1	2					
3.5						1						
4.0							2					
4.5								5		2		
5.0									1		1	1
5.5								1		1		
6.0						1	1		1			

$r = 0.747 \pm 0.024$

coefficient of 0.747 ± 0.024 is obtained. Compared in terms of the respective probable errors, this is as high as or slightly higher than the correlation between density and glume length.

The width of the kernels was not affected by the length of the kernels or by density. This density factor does not seem to produce diminutiveness but to shorten along one axis only. The width of the kernels, whether taken laterally or dorsi ventrally, remaining practically the same, the shape of the kernels assumes a spheroid form among the dense segregates and a long spindle form among the lax plants.

Since density is correlated with length of glume and length of kernel, it is obvious that in this material there is also a direct correlation between length of glume and length of kernel.

RELATION OF DENSITY OF RACHIS TO DENSITY OF RACHILLA

A rachilla is the rachis of a spikelet, and branches out from the main rachis. A spikelet may have three or more rachilla internodes; the basal one is very short, but toward the terminal part of the spikelet the internodes elongate and then shorten again.

It is practically impossible to measure the average rachilla internode length. For comparative purposes, however, the relation of density to average rachilla internode length can be determined indirectly by noting the extent of the protrusion of the fertile glumes of the florets. The relative distance between the fertile glumes of the first and the third floret on different wheat heads indicates their relative rachilla internode length, as is illustrated in figure 85.

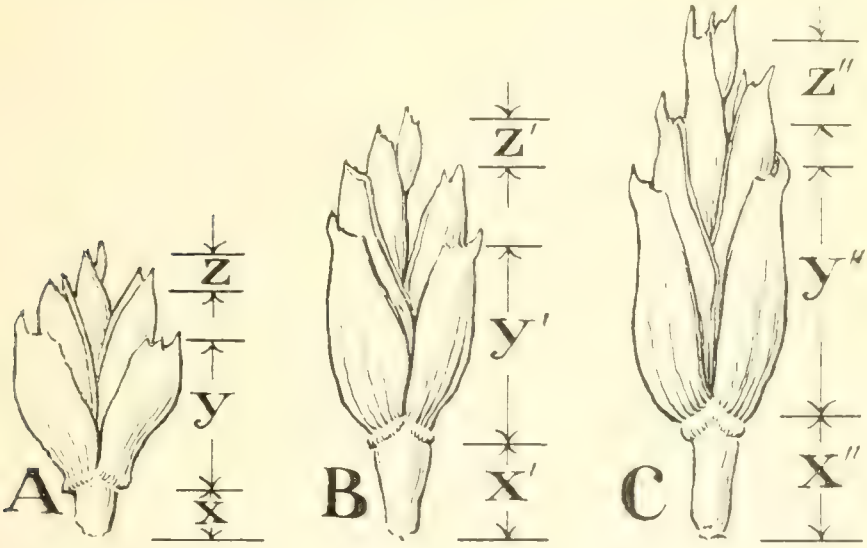

FIG. 85. SPIKELETS OF SPELTS OF VARYING DEGREES OF DENSITY, SHOWING RELATION OF INTERNODE LENGTH (X, X′, AND X″) TO LENGTH OF STERILE GLUMES (Y, Y′, AND Y″) AND RELATIVE RACHILLA INTERNODE LENGTH AS DETERMINED BY DISTANCE BETWEEN THE TIPS OF THE FERTILE GLUMES OF THE FIRST AND THIRD FLORETS (Z, Z′, AND Z″)

To bring out the correlation between rachis and rachilla internode length it is necessary to find a population comprising wheat plants of the same species which are segregating into dense and lax forms.

Dense and lax spelt plants of series 13255a-15 are reprersented, respectively, in *A* and *B* of figure 85. The illustration shows that the laxer was the form, the more did the florets protrude above the two sterile glumes. In figure 85, *C*, is represented the appearance of a synthetic spelt of un-

usual length derived from a *durum* x *vulgare* cross. It shows a further increase in rachis internode length, together with a relative increase in glume length.

These observations, which unfortunately cannot be presented in the usual form of a correlation table, indicate that *C*, the factor for compactness, shortens also the length of the rachillae or that of their internodes.

THE FACTOR FOR SPELTING ACTING AS A MODIFIER FOR THE DENSITY FACTOR

Density, like squareheadedness, is affected to a large extent by the presence of the spelt factor. In series 13255a, which represents a cross between White Spelt and Dale Gloria (Plate LXVII, upper, 4 to 12), there is but one spelt factor. Spelts and *sativums* segregate in this cross in the simple monohybrid ratio of 3 spelts of all grades (heads 6, 7, and 8) to 1 *sativum* (which includes *compactum* [heads 9 and 10], squareheads [head 11], and *vulgare* [head 12]). In a cross in which one of the parents is a spelt, the inheritance of density cannot be studied if all the plants are classified according to density alone, for, as will be seen, in the presence of the factor for spelting the factor for density does not produce compactness in the same degree as it does in the absence of the spelt factor. Therefore, in determining the mode of inheritance in such cases, it is necessary to take into consideration both the degree of spelting and the density, and in interpreting the data the density curves of the spelt and those of the *sativums* should be examined separately.

The difference in density of the spelt and the *sativum* form may be best illustrated by the density curves of the progeny of the two F_2 plants, one of which was homozygous dense and the other was homozygous lax, but both of which segregated into spelts and *sativums*. The relative density of spelts and *sativums* is shown in table 34. The plants of 13255a-26 are segregates from the Dale Gloria x White Spelt cross. They are all homozygous dense, but are derived from F_2 plants heterozygous for the spelting character. If *S* stands for the spelting factor and *C* for compactness, the F_3 progeny of line 13255a-28 consists of *SSCc*, *Sscc*, and *sscc* individuals, while 13255a-26 consists of *SSCC*,

TABLE 34. COMPARISON OF DENSITY OF SPELT AND SATIVUM SEGREGATES OF TWO F_3 PROGENIES, ONE HOMOZYGOUS DENSE BUT HETEROZYGOUS FOR SPELTING, THE OTHER HOMOZYGOUS LAX BUT HETEROZYGOUS FOR SPELTING
(Series 13255a, Dale Gloria x White Spelt)

Pedigree	Type	Average internode length (in millimeters)																				Number of plants	Difference between means
		1.3	1.5	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	Mean		
-26	Homozygous dense																						
	Spelt		1	8	6	3	1	3	2					..		..	..	..	..	..	2.00	24	
	Sativums	2	5	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.57	12	0.43
-28	Homozygous lax																						
	Spelt										1	1	2	2	5	7	2	7	4	4	4.22	35	
	Sativums	....	..	..	..	..	..	3	7	6	1	..	..	..	..	..	..	..	..	..	2.76	17	1.46

SsCC, and *ssCC* plants. The mean internode length of the lax spelts, as shown in table 34, was 4.22 millimeters; that of the *sativums* was 2.76 millimeters, showing a difference of 1.46. Of the plants homozygous for the density factor, the dense spelts had a mean internode length of 2.00 millimeters and the dense *sativums* one of 1.57, showing a difference of 0.43 millimeter.

From these results it is seen that, although the internode length of the spelts can be shortened by the introduction of the *C* factor, the presence of the *S* factor tends to interfere with the effect which a known *C* factor would otherwise produce.

The relation of the *S* factor to density is the same as the relation of this same factor to squareheadedness. It has already been shown that the presence of factors for squareheading have a very slight effect on the heads that carry the factor for spelting.

THE SYNTHETIC PRODUCTION OF TRITICUM COMPACTUM

Triticum compactum, as has already been shown, is but a form of *Tr. sativum*, which carries an additional factor or factors for compactness. The results of crosses between different species show that this same factor can be carried as well by any of the other species of Triticum. In fact, there will be found in commercial strains species that carry density factors, though not necessarily the same factor. Many forms of *durum*, and especially of *dicoccum*, carry a density factor. When these are crossed with a lax *vulgare* form, compact forms invariably appear in varying proportions, and, depending on the genotypic forms of the plant, some of these compact forms breed true while others segregate.

In order to produce compact forms, it is not necessary that one of the parents should be a dense form. If the plant is carrying an inhibiting factor besides the factor for density, it may appear lax although it has the potentiality of producing dense forms. Thus, Black Bearded Spelt, which has been used by the author, is perfectly lax, but when crossed with *vulgare* it produces lax spelts in the F_1, and in the F_2 an appreciable number of perfectly dense forms. The White Winter Spelt, on the other hand, produces no compact forms. The Black Bearded Spelt, then, carries a factor for compactness and also an inhibiting factor. Certain

forms of *turgidum*, *durum*, and even *polonicum* also have the ability to produce dense types in the F_2.

The writer has had no experience with *vulgare* crosses which have produced compact forms in the F_2; and unless the inhibiting factor is closely linked with the factors producing a certain specific form, it seems possible that certain *vulgare* forms will be met with which, although carrying the density factor, will be lax because of the presence of an inhibiting factor.

The mode of inheritance of density in some species crosses is very complex, because new specific forms arise in such crosses, each of which is affected in a peculiar way by the density factor. Besides factors for inhibition, many modifiers also may be involved. Often irregularities are produced by the failure of development or maturation of some forms which seem to carry combinations of growth factors that restrict growth or cause various anomalies. Before being able to analyze from a factorial point of view the inheritance of density in such crosses, it is necessary to know in what proportions the various specific forms segregate.

There are two cases which suggest that compact or semi-compact *vulgare* forms have been obtained through crossing two *vulgare* forms. De Vilmorin (1913) cites two instances in which lax forms produced dwarf forms. The dwarf plant, a photograph of which accompanies the text, appears to be a compact form much denser than the plant from which it mutated. It may also be possible that these cases were natural crosses with a *compactum* pollen, since segregation of other characters occurred also. Another case is that mentioned by Neethling (1918), in which tall *vulgare* forms crossed among themselves yielded dwarf forms. The latter behaved as recessives. The statement is made that the dwarf plants had short ears, but nothing is said about density. If these were *compactum* forms, the fact that these dwarf forms appeared in a proportion somewhat less than 25 per cent tends to lend support to the possibility that the parent which carried the density factor carried also a factor inhibiting the production of dense forms. Until more is learned about the behavior of the F_2 in the F_3, no definite explanation can be given to account for its mode of inheritance.

In Plate LXVII (lower) are shown a number of dense forms of different wheat species, most of these being synthetically produced in interspecific crosses. Some show both compactness and squareheadedness; others show one of these characters in the absence of the other. Körnicke (1885) has observed dense and squarehead varieties in other wheat species. He gives the following botanical varieties: *Triticum durum* Desf. var. *compactum* Sér., *Tr. polonicum* L. var. *compactum* Link., *Tr. polonicum* L. var. *quadratum* Sér., and *Tr. turgidum* L. var. *quadratum* Sér.

Density, or the excessive shortening of the rachis internodes, is not confined to the genus Triticum. Dense forms are common both in barley and in rye.

The question of the origin of *Tr. compactum* becomes simplified if it is recalled that this form may be produced when a *sativum* form is crossed with another wheat species, and also that natural crossing occurs not infrequently. Such being the case, one would expect *Tr. compactum* to be practically as old a form as any of the other species, and, so far as archaeological evidences go, cultivation of *Tr. compactum* has been traced as far back as the Stone Age. Buschan (1895) states that this compact form has been found in the remains of caves and lake dwellings and among other prehistoric relics in regions extending from Egypt to central Europe and to Sweden. According to Unger (1860), the culture of wheat has been traced back to the year 3623 B. C., and hence its origin must be older still.

If interspecific crosses between *vulgare* and other forms are able to produce compact forms, it seems that the first origin of *Tr. compactum* should have followed that of *Tr. vulgare*. Undoubtedly *Tr. compactum* has reappeared many times in the same manner, for the appearance of this form in interspecific crosses is rather common. *Tr. compactum* may be a mutational form of *vulgare*, although there is no dependable evidence regarding this possibility for *vulgare* wheats. There is a parallel example in the case of the rye known as "Heinrich-Roggen" (Hillmann, 1910: 579). This is a very compact form of rye which is said to have appeared in 1880 as a mutation on a single ear.

SUMMARY

The density studies reported herein were made primarily on the progeny of a number of crosses in which the dense parent was Dale Gloria (*Triticum compactum*), with an average internode length of about 1.41 millimeters.

Density was found to be dominant over laxness. The ratios obtained approached 3:1. The heterozygous forms were somewhat laxer than the homozygous dense forms, but by no means intermediate between the dense and the lax parents. The F_2 curves were bi-modal and discontinuous.

The F_3 plants showed various degrees of density within the dense and the lax classes. Proofs are given in the text showing that these variations are hereditary and are the result of the segregation of modifiers or of additional density factors capable of producing density only within short ranges.

Experimental evidence is cited suggesting that different density factors form allelomorphic series, and other evidence that they belong to multiple series.

Squareheadedness and density were found to represent two different characters. Hybrid progenies showed all types and grades of combinations between these two characters.

The process of squareheading was found to shorten the average internode length. The effect on density thus produced, however, is slight.

The phenotypic transmission of the squareheadedness of Dale Gloria is dependent on the type of the lax non-squarehead parent. In some crosses there was a large proportion of lax squarehead forms in the F_2, while in others there were none of these forms.

Although in F_2 progenies resulting from dense and lax crosses an almost perfect correlation exists between rachis length and density, these two characters are not necessarily correlated. Rachis length is the indirect product of average internode length and number of internodes. The correlation between density and rachis length becomes less and less as the difference between the number of internodes of the parental forms increases.

High degrees of correlation were found between average internode

length and length of culm, length of sterile glumes, and length of kernels, and average rachilla internode length. These, together with other observations, show that density and the shortening of these other length characters are the result of a single dwarfing factor.

Plants exhibiting the spelt character are not as much affected by the density factor as are those that show *sativum* characters.

Compact forms may be produced by crossing a lax *sativum* with lax forms of other species. Dense forms may also appear occasionally in crosses where neither parent is a *sativum*. Compactness is not a characteristic of *sativum* forms; other species also may exhibit this character.

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